

CO₂ AND CH₄ EMISSIONS IN RELATION TO NUTRIENT CYCLING AND DECOMPOSITION IN A NEOTROPICAL PEATLAND, PANAMA

by

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Abstract

Tropical peatlands play an important role in the global carbon cycle, but little is known about the factors which regulate carbon dioxide (CO₂) and methane (CH₄) fluxes from these ecosystems. To improve our understanding of the potential impact of future changes in climate and/or land-use, this study aimed to quantify current fluxes of these gases from a large domed peatland, San San Pond Sak, in Panama and assess the influence of environmental factors. Three sites with differing dominant vegetation species (*Raphia taedigera*, *Camposperma panamensis* and *Cyperus* species) and nutrient status were investigated between February 2007 – September 2009 using a combination of *in situ* closed chamber gas sampling and *ex situ* headspace gas sampling to quantify current and potential gas fluxes from the peat surface and at depths of 2 m from the surface. Physical and chemical properties of the peat were determined concurrently. Laboratory experiments were carried out to investigate patterns of litter decomposition and microbial activity. Gas fluxes differed significantly between sites. CO₂ fluxes were greatest at the *C. panamensis* site (100–400 mg m⁻² h⁻¹), followed by the *R. taedigera* (74–352 mg m⁻² h⁻¹) and *Cyperus* sp. (59–294 mg m⁻² h⁻¹). The seasonal patterns associated with rainfall were similar for all sites, with the release of CO₂ being greatest during the dry season. CH₄ fluxes also varied between sites, but no seasonal variation was evident. CO₂ flux varied diurnally at the *C. panamensis* and *Cyperus* sp. sites, perhaps due a circadian rhythm in vegetation processes. CO₂ and CH₄ production occurred throughout the upper 2 m of the profile, both *in situ* and *ex situ*, with potential CO₂ fluxes of up to 1,000 mg m⁻² h⁻¹ being found in the surface layer. The peat became increasingly recalcitrant and P-limited with increasing depth. Measurements of litter decomposition and microbial activity indicated that the availability of labile substrates and nutrients differed between sites. In conclusion, CO₂ and CH₄ fluxes differed between sites experiencing similar environmental conditions, and were influenced by variation in environmental factors. Fluxes varied on both short- and long- timescales, but not at all sites. The magnitude of the gas fluxes was influenced by different environmental factors at each site, indicating that fluxes and the

most important driving variables vary dependent on surface vegetation even within a single peatland system. With regard to climate and/or land-use change, it was concluded that San San Pond Sak peatland would be sensitive to water table drawdown, with the likely outcome of increased CO₂ releases and the potential for CH₄ uptake, rather than release.

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Chapter 1. Introduction

Peatlands occur throughout the World and occupy c. 3 % of the land surface (Maltby and Immerzi, 1993). Peatlands are formed when environmental conditions limit the decomposition of dead organic matter, often in combination with high net primary production, resulting in the accumulation of partially degraded plant material (Moore *et al.*, 2007). This accumulated material represents a relatively large carbon (C) store relative to the land area covered, and it is estimated that c. 525 Gt carbon (Maltby and Immerzi, 1993) is stored in peat Worldwide. Of this, c. 89 Gt C is thought to be stored in tropical peatlands, *ca.* 15 - 19 % of the global peat pool (Page *et al.*, 2011). However, the estimated quantity of C stored in tropical peatlands is based on limited data, mainly for Asian peatlands. Determination of the true extent of the land area in the tropics covered by peatlands and the depth of the peat deposits is difficult due to the scarcity of available information (Page *et al.*, 2011).

The rate of decomposition and hence C accumulation in peatlands is influenced by several factors including:

- (1) The degree of oxygenation of the peat as oxic conditions promote aerobic decomposition (Melling *et al.*, 2005a), whereas anoxic conditions promote anaerobic decomposition (Melling *et al.*, 2005b); the extent of aeration is strongly influenced by rainfall as this affects the level of the water table (Hadi *et al.*, 2005; Jauhainen *et al.*, 2005; Bloom *et al.*, 2010).
- (2) Low nutrient availability may reduce respiration rates and total nutrient content of the peat. The distribution of nutrients between the labile and recalcitrant fractions is important as both may govern nutrient availability to decomposer organisms (Chimner and Ewel, 2005).
- (3) The decomposition rate generally increases as the temperature of both the soil and air increase (Domisch *et al.*, 2006; Bloom *et al.*, 2010).
- (4) The dominant vegetation may also influence the decomposition rate, as the quality of fresh litter inputs (Chimner and Ewel,

2005) and root biomass, and hence root exudates and respiration, may differ greatly between species (Andrews *et al.*, 1999; Page *et al.*, 1999; Crow and Wieder, 2005).

Peatlands fall into three broad categories, boreal, temperate and tropical. Boreal and temperate peatlands are influenced primarily by season and the associated changes in environmental conditions (Williams and Yavitt, 2003). Tropical peatlands are not exposed to distinct seasonal changes in temperature and are instead thought to be primarily influenced by variation in rainfall between wet and dry seasons and associated variations in environmental factors e.g. position of the water table (Jauhiainen *et al.*, 2005).

Decomposition of dead organic matter is slow, but by no means absent, in peatlands, and both aerobic and anaerobic decomposition occurs depending on environmental conditions. Aerobic decomposition typically occurs when the peat is oxygenated i.e. when the water table is low, resulting in greater carbon dioxide (CO₂) production during dry periods (Jauhiainen *et al.*, 2005). Anaerobic decomposition by methanogenic bacteria only occurs when oxygen supplies are limited and methane (CH₄) is produced rather than CO₂ (Le Mer *et al.*, 2001). Anaerobic decomposition is a slower process than aerobic decomposition and often occurs at depth within the peat profile, below the water table where anaerobic conditions are maintained. However, up to 90 % of the CH₄ produced at depth (Bachoon *et al.*, 1992; Le Mer *et al.*, 2001) may be oxidised by methanotrophic bacteria as it diffuses from the anoxic horizons through the better oxygenated surface layer (Gurknecht *et al.*, 2006).

Though peatlands are generally regarded as C sinks, they have the potential to be future sources following changes in land-use, such as drainage and conversion to farmland (Furukawa *et al.*, 2005; Hooijer *et al.*, 2010) and/or climate change (Laiho, 2006). Under future climate change scenarios, tropical regions are predicted to become hotter and drier (Meehl *et al.*, 2007; Bloom *et al.*, 2010). In terms of tropical

peatlands, this has implications for drawdown of the water table, resulting in increased oxygenation of the peat. In combination with increased soil temperature, this may increase the decomposition rate of partially decomposed peat material at depth as well as new litter inputs, reducing the C storage capacity of tropical peatlands.

In order to accurately predict future tropical peatland emissions of CO₂ and CH₄ it is necessary to understand the processes involved in their production and factors that influence them. This study aims to quantify the fluxes of CO₂ and CH₄ from the undisturbed San San Pond Sak peatland and the influence of environmental factors on the magnitude of these fluxes.

Chapter 2 Literature review of control on Carbon dioxide and Methane production in peatlands

2.1 Peatlands and carbon storage

2.1.1 Global distribution of peatlands

The extent of global peatland coverage has been estimated in the range of $3,880 \times 10^3$ to $4,080 \times 10^3$ km² by Maltby and Immirzi (1993) although they acknowledge that this is likely an underestimate and as such an estimate by Bridgham *et al.* (1996) of $5,961 \times 10^3$ km² is probably closer to the true extent of peatland area.

Of the global peatland area, the estimates of peatland in tropical regions vary. Maltby and Immirzi (1993) estimated tropical areas at 333,820 - 497,120 km². This is slightly lower than more recent estimates such as that by Page *et al.* (2011) in which tropical peatland area was estimated between 387,201 - 657,430 km² with a best estimate of 441,025 km² which fell within the range estimated by Maltby and Immirzi (1993). Tropical peatlands represent *ca.* 11 % of the global peatland area and contain *ca.* 89 Gt of carbon (Page *et al.*, 2011).

The majority of peatlands are located in temperate and boreal regions with estimates in the range $3,460 \times 10^3$ to $3,589 \times 10^3$ km² presented by Gorham, (1991) and Maltby and Immirzi, (1993). This represents *ca.* 89 % of global peatlands.

2.1.2 Depth of peat deposits

Peatlands fall into three broad categories determined by latitudinal position. They are; boreal, temperate and tropical. The location of a peatland determines the environmental factors that will potentially affect the C storage capacity and what applies to one category will not necessarily apply to the others, for example, permafrost melting in boreal peatlands or monsoons in tropical peatlands. This means that whilst the

fundamental mechanisms of ecosystem functioning will be similar across peatland types, the primary factors that influence them may differ.

Tropical peatlands form deep peat deposits in comparison to temperate and boreal peatlands. Asian peatlands are thought to have the deepest peat deposits of the tropical regions. Extensive studies in Kalimantan, Indonesia have generally found that peat deposits are in the range of 0.5 - 11 m (Page *et al.*, 1999; Shimada *et al.*, 2001; Hope *et al.*, 2005). Some studies have found deposits of greater depths including 13.7 m in a coastal peatland of West Kalimantan (Shimada *et al.*, 2001). In Eastern Kalimantan deposits of up to 16 m were found by Hope *et al.* (2005). In comparison, other tropical peatlands have so far been found to be shallower than those of SE Asia. For example, Phillips *et al.* (1997) found peat deposits in the range of 0.5 - 8 m in San San Pond Sak peatland, Panama. Lahteenoja *et al.* (2009) found deposits of up to 5.9 m in Peruvian Amazon peat deposits. When all tropical regions were considered Page *et al.* (2011) estimated the majority of peat deposits to be in the range of 0.5 - 9 m.

Temperate peatlands have deposits that are typically in the range of 0.5 - 4.0 m. For example, Buffam *et al.* (2010) found that the majority of peat deposits in Wisconsin and Michigan fell between 0.1 - 4.0 m. In an Irish blanket bog Laine *et al.* (2007) found peat deposits of 2 - 3 m. Plado *et al.* (2011) found peat of up to 4.0 m depths in East Estonia. Not all peat depths were found to be lower than in tropical peatlands, some exceed the general majority of depths seen in tropical peatlands, for example, peat deposits of up to 14.6 m were found in Wisconsin and Michigan, USA in a study by Buffam *et al.* (2010). Peat depths of this extent are the exception rather than the norm in temperate peatlands.

Boreal peatlands tend to have the shallowest peat deposits compared to temperate and tropical peatlands. Some boreal locations were found to be comparable to temperate peatland depths, for example, Sheng *et al.* (2004) found peat deposits of 1 - 4 m depth in West Siberia. This was comparable with depths of ca. 0.3 - 4.5 m found in Finland by Silvola *et*

al. (1996). Other studies such as that by Plug (2003) found shallow deposits of < 2 m in Northwest Alaska. Slightly greater depth ranges were found in Northern Sweden of 0.5 - 3.0 m by Nilsson and Bohlin (1993). Deeper peat deposits seldom occur, though there are exceptions, for example, Silvola *et al.* (1996) found one location in Finland of 6 - 7 m depth. No peat deposits comparable to the deepest tropical deposits have been found in boreal peatlands.

Therefore although tropical peatlands cover a smaller land area the potential for extensive carbon stores is evident when considering the relatively greater depths of tropical peat in comparison to temperate and boreal peatlands.

2.1.3 Rate of carbon accumulation in peatlands

Peatlands are formed when environmental conditions promote slow rates of decomposition; this is often combined with a high rate of Net Primary Production (NPP) and results in the accumulation of partially decomposed plant material in the form of peat deposits (Moore *et al.*, 2007).

2.1.3.1 Historical carbon accumulation in peatlands

Historically peat accumulation/degradation rates are likely to have varied with the climate, so for periods of favourable conditions there were greater carbon accumulation rates. However, when dating peat it is important to remember that absence of peat of a certain age is not necessarily an indication of a slow accumulation rate, but could instead be indicative of peat degradation after formation. For example, Page *et al.* (2004) found in Indonesia, that the carbon accumulation rates alternated from periods of rapid accumulation (2 - 2.55 mm peat yr⁻¹) to slow or standstill periods (0 - 0.6 mm peat yr⁻¹). The highest carbon accumulation rate was found to be 74 mg C m⁻² yr⁻¹ at ≈ 24, 000 yr before present (BP) and the lowest rates at ≈ 12,000 - 13,000 yr BP at 1.3 g C m⁻² yr⁻¹. From this data two time periods were identified as being conducive to peat formation in Indonesia, they were the lead up to the last glacial maximum (LGM) 36,000 - 21,000 yr BP and the last glacial-interglacial transition

period 13,000 - 10,000 yr BP. This was supported in part in a study by Anshari *et al.* (2001) in which they found peat accumulations rates in West Kalimantan decreased in the time periods closer to the LGM, though it is speculated that this low accumulation may be due to oxidation in subsequent years as a result of climatic shift in favours of degradation processes.

Aucour *et al.* (1999) found in the Rusaka swamp in Africa a similar decrease in carbon accumulation rates during $\approx 13,600 - 12,000$ yr BP as well as during $5,500 - 1,600$ yr BP. These time periods are thought to represent drier climatic conditions. Carbon accumulation rates found by Aucour *et al.* (1999) ranged between $20 - 200 \text{ mg C m}^{-2} \text{ yr}^{-1}$, which were generally greater than those found in Indonesian peatlands (Page *et al.*, 2004).

From an analysis of available data, Dommain *et al.* (2011) found that during the Early Holocene, rapid sea-level rise lead to the initiation of many coastal peat domes in Kalimantan, however, inland peat formations in Indonesia were typically initiated in the period $29,000 - 21,000$ yr BP and are some of the oldest tropical peat deposits.

In contrast, the peat deposits of Central and Southern America are typically younger than those of Asia, for example, Phillips *et al.* (1997) used radiocarbon dating to suggest that the Changuinola peat deposit in Panama was initiated $\approx 4,000$ yr BP. Garcia *et al.* (2004) found that peat deposit initiation in the Jacarei deposits in Brazil was $\approx 9,700$ yr BP and that in Venezuela peat formation in the central and northwestern delta plain of the Rio Grande was found to have initiated $<3,000$ yr BP in response to prior sea-level changes during the Holocene.

Generally it can be seen that peat deposits present in the tropical Americas are younger in age than those of Africa or Asia. However the absence of older peat deposits does not preclude the suggestion that there may have been peat deposits formed during similar time periods as

the oldest Asian peats, but that instead shifting climates may have caused older peat deposits to degrade.

2.1.3.2 Current carbon accumulation in peatlands

The rate of carbon accumulation in peat deposits is greatest in the tropics, likely due to high NPP. Though there is a wide range of accumulation rates that have been measured in different peatlands. For example, Chimner and Ewel (2005) estimated carbon accumulation on the Island of Kosrae in Micronesia at $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ which is at the higher end of carbon accumulation rates in the tropics. The majority of measurements fall below $100 \text{ g C m}^{-2} \text{ yr}^{-1}$. In central Kalimantan for example, carbon accumulation rates were determined to be $31.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average by Dommain *et al.*, 2011. However, Page *et al.* (2004) suggest a current carbon accumulation rate of $84.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ which decreases to $56.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ when the past 500 years are considered. Coastal peatlands in Kalimantan were also considered by Dommain *et al.* (2011) with a reported carbon accumulation rate of $77 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average. Comparable C accumulation rates were reported in Peruvian Amazon peatlands by Lahteenoja *et al.* (2009), with accumulation rates ranging from $39 - 85 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Some carbon accumulation rates from temperate peatlands are comparable with the majority of measured tropical accumulation rates. For example, Craft and Richardson (1993) found accumulation rates in the range $54 - 161 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the North and Central Florida Everglades. Though the C accumulation rate can vary dependent on the types of peatland, as shown by Craft *et al.* (2008), when investigating peatlands between South Florida and Minnesota ($26 - 47^{\circ} \text{ N}$). Bog peatlands were found to have carbon accumulation rates, that were greater than typical tropical rates, at $132 - 198 \text{ g C m}^{-2} \text{ yr}^{-1}$. However fen peatlands had accumulation rates in the range $19 - 46 \text{ g C m}^{-2} \text{ yr}^{-1}$, lower than typical tropical accumulation rates. Anderson (2002) also found carbon accumulation rates that were lower than those of tropical peatlands in a bog in North-West Scotland, with a long term average accumulation of $21.3 \text{ g C m}^{-2} \text{ yr}^{-1}$. Roulet *et al.* (2007) found a similar carbon accumulation

rate of $21.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average in a peatland located in Ottawa Canada.

Carbon accumulation rates in boreal peatlands are generally lower than those found in temperate and tropical peatlands. Robinson and Moore (1999) found in a range of boreal Canadian peatlands, carbon accumulation rates that fell between $13.3 - 21.8 \text{ g C m}^{-2} \text{ yr}^{-1}$. Slightly lower rates were found in West – Central Canadian peatlands at $12.5 - 12.7 \text{ g C m}^{-2} \text{ yr}^{-1}$ by Sannel and Kuhry (2008). Substantially lower rates at $6.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ were found by Turunen and Turunen (2003), in a Canadian peat bog. In comparison, carbon accumulation rates found in Finland had a greater degree of overlay with the range of rates found in temperate and tropical peatlands. For example, Turunen *et al.* (2002) found accumulation rates in the range $15.4 - 35.3 \text{ g C m}^{-2} \text{ yr}^{-1}$. Whilst Ukonmaanaho *et al.* (2006) found in an ombrotrophic bog in Hietajarvi, Finland, substantially greater carbon accumulation rates at $32.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ on average. This is a greater accumulation rate than some areas of the tropics, so it can be seen that whilst accumulation rates are typically greatest in the tropical regions and decrease with latitude, this is not always the case.

2.1.3.3 Factors other than climate affecting carbon accumulation in peatlands

Carbon accumulation can be affected by processes other than decomposition. The most prominent of which are land-use change and fire.

Land-use change is an important factor relating to the carbon stores of tropical peatlands. One of the most important factors influencing peatlands is the soil moisture status, often inferred *via* the water table (WT) depth below or above the peat surface (*cf.* section 2.2.1) and typically when peatland is converted to other land uses the peatland is either drained or WTs are artificially controlled, with a subsequent impact on surface gas fluxes. For example, Hooijer *et al.* (2006) estimated that in 2006, 632 Mt CO_2 was emitted from drained peatlands in SE Asia (with a

range of 355 - 855 Mt CO₂). Peatlands that are drained or WT controlled are often used as farm land. Sago palm plantations are particularly common in SE Asia, Sago palm plantations need high WTs, so land that was previously peat is ideal. When used to produce commercial products fertilisers would commonly be applied, this can also affected gas fluxes, for example, Watanabe *et al.* (2009) found in the Riau Province of Indonesia, that fertiliser application on Sago palm plantation during the rainy season increased CH₄ flux from *ca.* 0.05 mg C m⁻² h⁻¹ (no fertiliser) to *ca.* 3.10 mg C m⁻² h⁻¹ with fertiliser application. Sago palm plantations as a CH₄ source was also found by Melling *et al.* (2005b), in Sarawak, Malaysia, with an annual carbon loss in the form of CH₄ of *ca.* 180 mg C m⁻² yr⁻¹ compared to *ca.* 18 mg C m⁻² yr⁻¹ in a mixed peat swamp forest in the same region. This was thought to be due to the high WTs required for Sago Pal plantations increasing the susceptibility of these areas to flooding and favouring anaerobic respiration. Conversely the conversion to Oil palm plantation resulted in a CH₄ sink site, with an uptake rate of 15 mg C m⁻² yr⁻¹, again thought to be due to WT depth (in this case increased depth below the peat surface) together with the peat temperature (conversion to plantation lead to greater exposure of the peat surface and therefore peat temperature increased).

The effect of land-use change to plantation on CO₂ flux on first look appears to be negligible. Some studies have found no significant difference in CO₂ flux between undisturbed peatlands and peatlands that have been converted to plantation. For example, Page *et al.* (2011) in the lowlands of Central Kalimantan, Indonesia estimated that CO₂ fluxes from a non-drained peat forest were 3713 ± 520 g m⁻² yr⁻¹ compared to flux from a drained peat forest site of 3719 ± 383 g m⁻² yr⁻¹ (however under dry conditions the drained forest site had greater CO₂ fluxes than the non-drained site due to WT drawdown). Other studies have found that indisturbed peat sites produced higher CO₂ fluxes than those peat sites that had been converted to plantations, for example, Melling *et al.* (2005a) found in Sarawak, Malyasia, that a mixed peat swamppl forest had a CO₂ flux of *ca.* 100 - 533 mg C m⁻² h⁻¹ compared to an oil palm plantation *ca.* 63 - 245 mg C m⁻² h⁻¹ and a Sago palm plantation *ca.* 46 -

335 mg C m⁻² h⁻¹. It was suggested that these differences in CO₂ flux rates were driven by the decreased biomass and productivity of the plantations (compared to peat forest) and the subsequent decreased root biomass and therefore root derived CO₂ from root respiration. The extent of land-use change can also affect the potential CO₂ flux. Jauhiainen *et al.* (2008) compared a drainage affected, selectively logged peat forest with a drained, deforested and burnt peatland in Central Kalimantan. They found that the selectively logged forest had higher CO₂ fluxes (400 - 1600 mg m⁻² h⁻¹) compared to the deforested and burnt peatland (0 - 700 mg m⁻² h⁻¹; although this does not include the CO₂ emissions from the peat fires).

Whilst plantations may appear to have similar or lower CO₂ fluxes, the CO₂ produced from former peatlands is derived from the degradation of peat material (excluding the portion of CO₂ flux from root respiration) that is not being replaced by the formation of new peat material as in carbon accumulating peatlands, thereby reducing the carbon store of peatlands converted to alternate land-use.

Degraded peatlands, particularly those that have been drained, have been found to be more susceptible to fires (Miettinen and Liew, 2010) and hence large point emissions of carbon from the peat stores, for example, Page *et al.* (2002) found in Central Kalimantan, Borneo, that the 1997 fires burned 51.3 % of the mega-rice project (MRP) area (a degraded area, heavily influenced by anthropogenic clearing) in comparison to only 19.3 % of the peatlands outside the MRP. The present an overall estimate of 2.18 - 2.57 Gt C released from Indonesian peat fires in 1997.

Using satellite data, van der Werf *et al.* (2008) investigated the areas of Indonesia, Malaysia and Papua New Guinea and found strong links between the intensity of drought and carbon emissions from fires. They found that fire occurrences and carbon emissions were exponentially linked, with an increase in carbon releases with an increase in drought severity, for example, in Borneo in 2000, the dry season was short due to la Niña conditions, with 7 ± 3 Tg C yr⁻¹ estimated losses due to fires.

Compared to 2006, when there were El Niño conditions and an extended dry season, with an estimate of $236 \pm 106 \text{ Tg C yr}^{-1}$ losses from fires.

These studies show how land-use change and other anthropogenic influences can lead to enhanced degradation of peat material. These changes also link in together, as land-use change tends to result in the peatland becoming more susceptible to drought, which increases the risk of fires, leading to increased greenhouse gas emissions, which further enhance climatic change leading to drier conditions, which then further enhance drought and so on in a feedback loop.

2.1.4 Carbon dioxide and methane fluxes

There are two decomposition processes that dominate in peatlands; aerobic and anaerobic decomposition. Aerobic decomposition occurs in the presence of oxygen (O_2) and anaerobic when O_2 is absent.

2.1.4.1 Aerobic decomposition

Aerobic decomposition of organic matter occurs when conditions within the peat are oxic. Microbes within the peat produce extracellular enzymes that break down plant fibers (cellulose, hemi-cellulose and lignin) by a combination of hydrolysis and oxidation, hence why this process occurs only under oxic conditions. The final products of aerobic decomposition include CO_2 , dissolved organic carbon (DOC), inorganic and organic nutrients and peat humus (Melling *et al.*, 2005a; Huissteden *et al.*, 2006; Bragazza *et al.*, 2009).

2.1.4.2 Anaerobic decomposition

Anaerobic decomposition occurs when peat conditions are anoxic. It is a four stage process, the first three stages are concerned with the breakdown of large complex molecules into relatively simple compounds by hydrolysis, acidogenesis and acetogenesis processes (Le Mer and Roger, 2001). The final stage of decomposition is methanogenesis. The simple compounds produced by the prior processes (namely H_2 , CO_2 and

acetate) are utilised by methanogenic bacteria which produce CH₄ as an end product of anaerobic decomposition (Segers, 1998; Le Mer and Roger, 2001). Methanogenesis only occurs when there is no oxygen present and typically when redox potentials are < -200 mV (Le Mer and Roger, 2001).

CO₂ and CH₄ fluxes from the peat surface are often used as a measure of decomposition processes. CO₂ and CH₄ are produced within the peat profile and diffuse upwards before release to the atmosphere at the peat surface.

2.1.4.3 Carbon dioxide

Global estimates of soil CO₂ emissions are in the region of 68,000 - 77,000 Tg C y⁻¹ (Schlesinger, 1977; Raich and Schlesinger, 1992; Raich and Potter, 1995).

Measurements of CO₂ emissions from boreal, temperate and tropical peatlands can be found in table 2.1. Generally CO₂ emission rates are greatest in tropical regions, although emission rates are highly variable and affected by local conditions, for example, Murayama and AbuBakar (1996) found fluxes in the range of 93 - 486 mg m⁻² h⁻¹ in Malaysia, whereas a study by Melling *et al.* (2005a) found a greater range and a higher magnitude of CO₂ flux at 366 - 1953 mg m⁻² h⁻¹. This represented the higher magnitudes of CO₂ flux, with the majority of measurements in the range of 200 - 500 mg m⁻² h⁻¹.

Temperate peatlands have CO₂ fluxes that are similar in mean magnitude to those of tropical systems, but have a smaller range and the greatest fluxes measured in temperate peatlands were lower than those measured in tropical peatlands. Lund *et al.* (2007) found some of the highest CO₂ fluxes measured in temperate peatlands ranging between 288 - 756 mg CO₂ m⁻² h⁻¹. Comparable fluxes were measured by Alm *et al.* (1999) in eastern Finland in the range 37 - 641 mg m⁻² h⁻¹. Fluxes from a temperate peatland in Scotland were within the same range but were generally of a greater magnitude (331 - 601 mg m⁻² h⁻¹).

The magnitude of CO₂ fluxes of boreal peatlands have been shown to be highly variable, for example, some measurements of < 1 mg m⁻² h⁻¹ were found by Clair *et al.* (2002) and Crow and Wieder (2005) in Canadian peatlands and in northern Finland by Makiranta *et al.* (2009). In contrast, other boreal peatlands had CO₂ fluxes that were *ca.* 80 - 300 mg m⁻² h⁻¹ e.g. Alaskan peatland by Oechel *et al.*, (1993; 1 - 163 mg m⁻² h⁻¹), Northern Finland by Silvola *et al.*, (1996; 78 - 259 mg m⁻² h⁻¹), and in Canadian peatlands by Bubier *et al.*, (2003; 86 - 346 mg m⁻² h⁻¹).

2.1.4.4 Methane

Estimates of rates of CH₄ emissions from peatlands over all latitudes are typically several orders of magnitude lower than CO₂ emission estimates (Table 2.1). In some peatlands CH₄ is not emitted from the peat and active uptake from the atmosphere is seen instead. This can occur across all organic soil types and is dependent on the local environmental conditions (Sjogersten and Wookey, 2002; Inubushi *et al.*, 2005).

It has been strongly suggested that the majority of CH₄ emissions to the atmosphere, from wetlands, are from tropical regions (Bartlett and Harriss, 1993). A study by Bloom *et al.* (2010) suggests that as much as 58 % of CH₄ emissions from wetlands is from the tropics and as little as 2 % from systems located in boreal regions. This was similar to estimates made by Bartlett and Harriss (1993). Conversely some studies, such as that by Couwenberg *et al.* (2010), disagree and found instead that tropical peatland CH₄ emissions were lower than those of boreal and temperate peatlands.

Measurements of tropical peatland CH₄ fluxes have found ranges of -0.1 to 35 mg m⁻² h⁻¹. Though CH₄ flux at the higher end of the range is usually attributed to the flux rate of rice paddy field. For example, Hadi *et al.* (2002, 2005) found CH₄ fluxes between 3.5 - 14 mg m⁻² h⁻¹ in a rice paddy in SE Asia. Flux measurements by Furuwaka *et al.* (2005) in a rice paddy field also in SE Asia had average flux of 35 mg m⁻² h⁻¹. Fluxes from natural peatlands are typically lower and on Indonesian peatlands were found to be *ca.* 1.1 mg m⁻² h⁻¹ in Indonesia by Inubushi *et al.* (1998) and

a lower CH₄ flux ranging from -0.1 to 0.35 mg m⁻² h⁻¹ by Jauhiainen *et al.* (2005). Estimates from Malaysia were of a smaller magnitude at -0.006 to 0.011 mg m⁻² h⁻¹ (Melling *et al.*, 2005b). whilst CH₄ fluxes in Panama were comparable at 0 - 1 mg m⁻² h⁻¹ (Sjogersten *et al.*, 2010).

Temperate peatlands appear to have a greater range of CH₄ flux than tropical peatlands, with fluxes typically falling between 0 - 5 mg m⁻² h⁻¹ in studies by Alm *et al.* (1999). Laine *et al.* (2007) found a slightly lower range of flux between 0.083 and 2.21 mg m⁻² h⁻¹ in a lowland Irish bog.

Boreal CH₄ fluxes are thought to potentially be the smallest. This was confirmed by Whalen and Reeburgh (2000) who found fluxes of 0.0375 mg m⁻² h⁻¹ in temporarily saturated peatlands in Alaska. This rose to 2.875 mg m⁻² h⁻¹ when permanently flooded peatlands were studied. Clair *et al.* (2002) found very low fluxes in Eastern Canada between 0 and 0.0000043 mg m⁻² h⁻¹.

Current literature on C cycling in boreal and temperate peatlands is extensive. The C storage, release and the controlling factors of these processes are well documented. The primary factor that influences the C storage of these peatlands is the season (spring, summer, autumn, winter) and the associated variations in environmental conditions (Williams and Yavitt, 2003). Tropical peatlands are not exposed to the same distinct seasons as boreal and temperate peatlands. They are instead thought to be primarily influenced by rainfall (and associated variations in environmental factors) resulting in pronounced wet and dry

Table 2.1 Carbon dioxide and methane fluxes from tropical, temperate and boreal peatlands various locations
UD = Undifferentiated

Category	Location	Land cover	Peatland type	Study considerations	Sampling method	Emissions measured	Carbon Dioxide (mg m ⁻² h ⁻¹)	Methane (mg m ⁻² h ⁻¹)	Reference
Tropical	Indonesia	<i>Shorea albida</i>	Swamp forest peat	Undisturbed site adjacent to Sago palm plantation	Closed chamber for 1 h	UD	n/a	1.1	Inubushi <i>et al.</i> , (1998)
Tropical	South Kalimantan Kosrae, Micronesia	Rice	Paddy field	Cultivated peatland	Closed chambers, 12 sample plots	UD	n/a	3.5 - 14	Hadi <i>et al.</i> , (2002, 2005) Chimner (2004)
Tropical		<i>Terminalia carolinensis</i>	Forested Lowland peat	Maximum of 4 sampling dates over 1 year	Closed chamber	UD	340 - 402	n/a	
Tropical	Maui, Hawaii	Common species include: <i>Deschampsia nubigena</i> , <i>Carex alligata</i>	Montane peat bog	Maximum of 4 sampling dates over 1 year	Closed chamber	UD	131 - 187	n/a	Chimner (2004)
Tropical	Sumatra, Indonesia	Rice	Paddy field	Cultivated peatland	Closed chamber	UD	n/a	35	Furuwaka <i>et al.</i> , (2005)
Tropical	Central Kalimantan	Mixed type forest	Peat soil	Hummocks and hollows	Closed chambers on surface for hummocks and metal collars for hollows	UD	50 - 550	-0.1 - 0.35	Jauhiainen <i>et al.</i> , (2005)
Tropical	Sarawak, Malaysia	Mixed forest	Peat soil	Three samples from each plot per month	Closed chamber	UD	366 - 1953	n/a	Mellling <i>et al.</i> , (2005a)
Tropical	Sarawak, Malaysia	Mixed forest	Peat soil	Three samples from each plot per month	Closed chamber	UD	n/a	-0.006 - 0.011	Mellling <i>et al.</i> , (2005b)

Table 2.1 continued

Category	Location	Land cover	Peatland type	Study considerations	Sampling method	Emissions measured	Carbon Dioxide (mg m ⁻² h ⁻¹)	Methane (mg m ⁻² h ⁻¹)	Reference
Tropical	Central Kalimantan	Forested	Forest peatland	Selectively logged in 1990s	Continuous automated sampling from 6 chambers	UD	317 - 950	n/a	Hirano <i>et al.</i> , (2009)
Tropical	Indonesia Bocas del Toro Panama	Three sites, <i>Raphia taedigera</i> , <i>Camptosperma panamensis</i> and <i>Cyperus</i> sp. dominated	Domed peatland	Measurements from one month only	Closed chamber	UD	200 - 400	0 - 1	Sjogersten <i>et al.</i> , (2010)
Temperate	Eastern Finland	<i>Sphagnum fuscum</i>	Ombrotrophic peat bog	Sampling late May - mid-October. Exceptional water table drawdown during July and August	Closed chamber with metal collars	UD	37 - 641	0 - 5.34	Alm <i>et al.</i> , (1999)
Temperate	Southern Sweden	Dominated by <i>Sphagnum magellanicum</i>	Ombrotrophic bog	12 point measurements only	Laboratory Study of 12 peat monoliths	UD	n/a	8 - 27	Joabsson <i>et al.</i> , (1999) (Lab measurements)
Temperate	Kejimikujik, Eastern Canada	Mixed hardwood-softwood tree species	Forested peat wetland	Over 1 year only	Static chambers with metal collars	UD	0.0000253 - 0.00048	0 - 0.0000043	Clair <i>et al.</i> , (2002)
Temperate	County Kerry, Ireland	Mosses and vascular plants	Lowland bog	Biweekly to monthly sampling for 2 years	6 sampling plots with metal collars	UD	n/a	0.083 - 2.21	Laine <i>et al.</i> , (2007)

Table 2.1 continued

Category	Location	Land cover	Peatland type	Study considerations	Sampling method	Emissions measured	Carbon Dioxide (mg m ⁻² h ⁻¹)	Methane (mg m ⁻² h ⁻¹)	Reference
Temperate	Near Edinburgh, Scotland	Mosses	Peat soil	Water table drawdown > 35 cm	Static chambers, weekly sampling	UD	331 - 601	0.68 - 687	Dinsmore <i>et al.</i> , (2009) (Lab measurements)
Temperate	Finland	Forested	Peat soil	Re-forested after agricultural use	Static chambers	UD	0 - 0.0013	n/a	Makiranta <i>et al.</i> , (2009)
Boreal	Alaska	Various locations	Peat soil	Transect from Arctic ocean to Toolik Lake	Long-term, temperature controlled chamber	UD	1.4 - 162.5	n/a	Oechel <i>et al.</i> , (1993)
Boreal	Eastern Finland	Vegetation removed	Peat soil	Surface vegetation removed.	Non-closed chambers summertime. Closed chamber wintertime	Net emission	78 - 259	n/a	Silvola <i>et al.</i> , (1996)
Boreal	Canada	Dominated by ericaceous shrubs	Raised ombrotrophic bog	Vegetation emissions included	Closed chamber with metal collars	UD	86 - 346	n/a	Bubier <i>et al.</i> , (2003)
Boreal	Saskatchewan, Canada	<i>Sphagnum</i> mosses, ericaceous shrubs and sparsely distributed black spruce	Peat soil	Discontinuous permafrost zone	Laboratory Study with 40 peat cores	Net emissions	0.37 - 0.75	n/a	Crow and Wielder (2005)

seasons with implications for CO₂ and CH₄ production (Jauhiainen *et al.*, 2005).

The literature addressing C storage and release in tropical peatlands is less exhaustive, this is likely due to the often isolated nature of these peatlands and the difficulty in accessing them, meaning that detailed investigations are rare, but there are some notable exceptions (for example, Phillips *et al.*, 1997; Page *et al.*, 1999, 2004). This results in a dearth of knowledge which has implications for accurate estimates and predictions of C storage and release under current and future climate scenarios.

2.2 Factors effecting peat decomposition

2.2.1 Peat Hydrology

The hydrology of peatlands is a major controlling factor on the extent of CO₂ and CH₄ production within the peat in tropical wetlands (Hirano *et al.*, 2009). Hydrology is important not just because of its effect on gas production, but also for the influence it has on other peat factors, for example, Clair *et al.*, (2002) suggest that greater surface water runoff could cause increased dissolved organic carbon losses. Variations in DOC were also found by Moore *et al.* (2011) in Indonesian, with increased DOC concentrations during the wet season. Water table depth is often cited as an indication of the moisture status of the peat, the peat moisture status is important in determining the extent of decomposition processes within peat.

CO₂ is an end product of aerobic respiration. As such there is greater CO₂ production when the depth to water table below the peat surface increases. This is true for in categories of peatland. Examples in boreal peatlands are; Oechel *et al.* (1993) found greater carbon (C) losses of ca. 65 mg CO₂ m⁻² h⁻¹ under well drained conditions in comparison to flooded

conditions with C losses of *ca.* 14 mg CO₂ m⁻² h⁻¹, in the form of CO₂, in a peatland in Alaska. In Northern Finland, Silvola *et al* (1996) found that C losses in the form of CO₂ increased by *ca.* 4 mg CO₂ m⁻² h⁻¹ for each cm lowering of the water table below the surface. Examples from temperate peatlands include a study by Dinsmore *et al* (2009) who found from laboratory manipulations of water tables that CO₂ production was up to 155 mg CO₂ m⁻² h⁻¹ greater when the water table was at a depth of *ca.* 30 cm. In the subtropical Florida Everglades Debusk and Reddy (2003) found that CO₂ flux rate was *ca.* 27 mg CO₂ m⁻² h⁻¹, this increased to *ca.* 183 mg CO₂ m⁻² h⁻¹ when the water table drawdown was 15 cm. Examples from tropical peatlands include a study by Furukawa *et al.* (2005), that showed that a 10 cm drop in water table from the peat surface corresponded to a subsequent increase in CO₂ flux from 400 mg CO₂ m⁻² h⁻¹ to 595 mg CO₂ m⁻² h⁻¹ in peatlands in Indonesia. Also in Indonesia, Jauhiainen *et al.* (2005) found CO₂ flux to be virtually zero when the water table was 20 cm above the peat surface. This was found to increase to *ca.* 530 mg CO₂ m⁻² h⁻¹ when the water table decreased to *ca.* 80 cm depth.

The increase in CO₂ flux to the atmosphere found in response to dropping water tables can be in part attributed to the increasing O₂ concentrations in the peat with increasing water table depth. The periodicity and duration of flooding events can also influence the O₂ concentrations of the peat, for example, Laing *et al.* (2010) found in a Scottish peatland that was typically flooded, oxygen concentrations of zero by *ca.* 27 mm below the water table. This was compared with a Scottish peatland that had had greater occurrence and duration of dry periods with water table drawdown, and it was found that in this instance the oxygen concentration declined to zero at *ca.* 42 mm below the water table. Indicating that peatlands that experience more water table drawdown are likely to have increased O₂ concentrations to a greater depth than peatlands that are typically flooded. Askaer *et al.*, (2010) found results that were comparable when measuring oxygen in terms of percentage air saturation. In a temperate peatland in Denmark oxygen content was always < 2 % air saturation below the water table. When the water table was 49.8 cm below the peat surface oxygen content was 97 % air saturation at 5 cm

depth, 68 % at 20 cm depth and 2 - 5 % between 25 - 40 cm depths. This highlights the importance of the water table on the degree of aeration of the peat and the potential for CO₂ production *via* aerobic respiration.

There is the potential for water tables to fall below the peat surface to the point where the drawdown occurs to depths which cause water stress and decrease the rate of aerobic decomposition. Hirano *et al.*, (2007) found that CO₂ production was *ca.* 173 mg m⁻² h⁻¹ when the water table was 70 cm below the peat surface, however when water tables rose to *ca.* 10 - 20 cm depth then the CO₂ production rate increased to *ca.* 289 mg m⁻² h⁻¹ in a tropical peatland in Indonesia.

CH₄ is produced as an end product of anaerobic decomposition. Therefore the opposite tendencies to CO₂ production are seen i.e. as the water table draws down below the peat surface CH₄ production decreases. For example, Couwenberg *et al.* (2010) on performing a meta-analysis of available data from south-east Asia, found that CH₄ fluxes were zero when the water table was more than 40 cm below the peat surface. For water tables between 0 and 40 cm below the peat surface CH₄ fluxes fell between 0 and 0.5 mg CH₄ m⁻² h⁻¹ and fluxes were *ca.* 0 to 1.2 mg CH₄ m⁻² h⁻¹ when the water table was at or just above the peat surface.

CH₄ production is greatest when the water table is above the surface of the peat. This has been established through extensive studies, some examples of which are; Jauhiainen *et al.* (2005) found that CH₄ flux was *ca.* 2.2 mg m⁻² h⁻¹ when the water table was 20 cm above the peat surface of a peatland in Indonesia. They also found that the peatland switched to a CH₄ sink when the water table was > 60 cm below the peat surface, with uptake rates of *ca.* 0.1 mg m⁻² h⁻¹. CH₄ production was found to be greatest at high water tables in temperate peatlands as well, for example, Dinsmore *et al.* (2009) found that CH₄ flux was *ca.* 30 - 55 times greater when the water table was at the peat surface (range 0.011 - 0.191 mg m⁻² h⁻¹) compared to when the water table was 30 cm below the peat surface (range 0.00019 - 0.0058 mg m⁻² h⁻¹). Laine *et al.* (2007) found similar CH₄ flux patterns with *ca.* 1.88 mg m⁻² h⁻¹ with water tables

of 7 cm above the peat and *ca.* 0.42 mg m⁻² h⁻¹ when the water table was 15 cm below.

Alongside the study by Jauhiainen *et al.* (2005), other peatlands have been found to act as a sink rather than a source of CH₄ if the water table drawdown is sufficient. Frenzel and Karofeld, (2000), found in a temperate peatland in Estonia, that when the water table was *ca.* 15 - 20 cm below the peat surface CH₄ uptake was on average 0.02 mg m⁻² h⁻¹. The peatland did not become a source of CH₄ until the water table was *ca.* 1 - 2 cm below the peat surface, when CH₄ efflux was measured at *ca.* 0.27 mg m⁻² h⁻¹. In Indonesia Jauhiainen *et al.* (2008) found that peat would switch from being a distinct source of CH₄ to a sink at different depths dependent on the location sampled. As such one site switched when the water table was 25 cm below the peat surface and the other site when the water table was 12 cm below the surface. CH₄ uptake rates were between 0 - 0.15 mg m⁻² h⁻¹ and efflux rates were in the range 0 - 0.3 mg m⁻² h⁻¹, under the deeper and shallower water table, respectively. These studies all agree that peat can act as a CH₄ source as well as a sink dependent on the water table. However, an important point to consider in this context is that the CH₄ uptake rates were, in the majority of studies, much smaller than the rates of CH₄ efflux.

The uptake of CH₄ is caused by the oxidation of CH₄ to CO₂ within aerated peat by methanotrophic bacteria. This may also explain decreased surface emission of peat during periods of water table draw down. When the water table draws down, deeper peat below the water retains anoxic conditions and continues to produce CH₄. Inubushi *et al.* (1998) found that CH₄ production rates were *ca.* 1 mg m⁻² h⁻¹ for 0 - 20 cm below the water table in a peatland in Indonesia and rose to 340 mg m⁻² h⁻¹ at 28 - 40 cm below the water table. This was also seen in a Scottish peatland by Laing *et al.* (2010), where dissolved CH₄ was measured as an indication of CH₄ production below the water table. However, this study did not measure surface oxidation rates, so does not necessarily accurately reflect the surface emissions. Nedwell and Watson (1995) found in a Scottish peatland that oxidation in the surface layer was between 0 and 97 % of

CH₄ produced within the peat profile. Hornibrook *et al.* (2009) measured the rate of CH₄ oxidation in a temperate peatland in Wales and found oxidation rates in the range of 5 - 63 mg m⁻² h⁻¹. As such it can be inferred that the percentage of CH₄ produced within the peat profile that is oxidised to CO₂ will be dependent on the rate of CH₄ diffusion through the peat, the degree of aeration of the surface layer and the depth of the water table.

The water table level is relative to the surface of the peat, hence the microtopography of the peat is important, due to the formation of hummocks and hollows within peatlands. This means that portions of the surface can be flooded (hollows) whilst other parts have a water level below the surface of the peat (hummocks). The variation that this causes in CO₂ and CH₄ surface fluxes is well documented. Jauhiainen *et al.* (2005) found that during the wet season in a tropical peatland in Indonesia 65 - 80 % of the surface was water covered (hollows). When the ratio of hummocks to hollows was manipulated, calculations based on field measurements of surface fluxes, demonstrated that an increase in the ratio (i.e. increased hummock coverage) could potentially enhance CO₂ production and decrease CH₄ production. Hirano *et al.* (2009) also studied fluxes from hummocks and hollows and found that the relative water tables caused the same flux effects in hummocks and hollows. Both hummocks and hollows were found to have a sharp decrease in CO₂ flux rate when the water table was at depths of < 20 cm relative to the peat surface. Fluxes from the hollows were found to be of a lesser magnitude (between 475 - 792 mg CO₂ m⁻² h⁻¹) than the fluxes measured from hummocks (between 634 - 1,109 mg CO₂ m⁻² h⁻¹) when water tables were > 20 cm depth. The mean CO₂ flux rates in hollows were typically lower due to the higher water tables relative to those of the hummocks. This increased flooding in the hollows would influence the O₂ concentrations and decrease the aerobic decomposition rate resulting in the lower CO₂ flux rates relative to the hummocks. This suggests potentially high spatial variation in CO₂ and CH₄ in response to micropotography and the related water table levels relative to the peat surface.

As discussed above the majority of studies demonstrate that water table drawdown can promote extensive aerobic decomposition. However, Laiho *et al.* (2006) suggest that the short term effect of lower water tables is to increase the potential CO₂ efflux, but that on a longer timescale prolonged drawdown does not necessarily equate to continual high CO₂ efflux and that as the system adjusts and as labile C compounds in the deeper peat are exhausted, there may still be a net C accumulation.

It should also be noted that CH₄ flux measurements may be effected by ebullition (release of CH₄ bubbles) from the deeper peat, causing large point emissions of CH₄. The occurrence of CH₄ bubbles is well documented, for example, Tokida *et al.* (2005) found the presence of CH₄ in gas form throughout the profile in a Japanese peatland. They found ebullition to be unevenly distributed through the peat profile and that below the water table more than 50 % of the CH₄ was in gas form held in bubble form compared to an average of 60 % across the profile. Ebullition in peatlands is an important consideration as, though it is not a continual occurrence, CH₄ bubbles represent a significant release to the atmosphere so to omit large CH₄ measurements from data analysis may give false representation of the true extent of CH₄ release. Indeed, some studies have estimated that CH₄ bubbles can constitute 20 - 73 % of total CH₄ emissions. For example, Bartlett *et al.* (1990) found that in a flooded Amazonian forest *ca.* 47 % of the surface flux samples contained CH₄ that was transported through the profile *via* bubble ebullition, this accounted for more than 70 % of the CH₄ efflux at 98 mg m⁻² d⁻¹ compared to diffusive transport which accounted for 44 mg m⁻² d⁻¹ on average.

2.2.2 Temperature

The peat temperature controls the rate of decomposition and hence the production of CO₂ and CH₄. Temperature increases are generally positively correlated with rates of decomposition and hence gas production and have been extensively documented in boreal and temperate peatlands. Examples of temperature effects on decomposition in temperate peatlands include studies by Laine *et al.* (2007) and Dinsmore *et al.* (2009). In an

Irish lowland bog Laine *et al.* (2007) found that CH₄ flux was closely correlated with the peat temperature at a depth of 20 cm, on both an annual and diurnal basis. On average 0.21 mg CH₄ m⁻² h⁻¹ was produced when the temperature was *ca.* 8 °C. This rose to 1.17 mg m⁻² h⁻¹ when the temperature increased to *ca.* 13 °C. Dinsmore *et al.* (2009) also showed an effect of temperature increase on CH₄ emissions in moss peatland in Scotland. CH₄ flux increased from *ca.* 0.05 mg m⁻² h⁻¹ at 5 °C to *ca.* 200 mg m⁻² h⁻¹ at 9 °C (but only when the peat was flooded). The large variation in the magnitude of CH₄ flux and the response to temperature in two systems of similar latitude should be noted as an indication of the wide spatial variation in CH₄ flux. Concurrent with efflux measurement, organic matter losses have also been used to determine decomposition rates. Domisch *et al.* (2005) studied the decomposition of needle litter in a North Finland peatland. They found that at 5 °C *ca.* 55 % of the total mass was lost over 300 days, in comparison to *ca.* 90 - 95 % loss when the temperature was 15 °C.

It is typically considered that temperature variation is of greater influence in boreal and temperate peatlands than in tropical peatlands, as northern systems generally have greater temperature fluctuations with time. Makiranta *et al.* (2009) studied a peatland in Finland and found that at 0 °C there was virtually zero CH₄ production. When the temperature was increased to 20 °C they found that CH₄ production increased to *ca.* 0.6 g m⁻² h⁻¹ at 5 cm depth. Domisch *et al.* (2005) compared Northern and Southern Finland needle decomposition in peatlands and found that peatlands of higher latitudes were more sensitive to temperature changes than peatlands of a more temperate latitude. At 15 °C the Northern peatland had 95 % organic matter loss over 300 days whereas the Southern peatland had an 87 % loss. In tropical regions there is often very little temperature variation annually; however, even small variations can potentially impact upon peat processes. A study by Hirano *et al.* (2009) found in a tropical peatland in Central Kalimantan, Indonesia, that CO₂ flux varied in temperature response dependent on the microtopography of the peat surface. Hummocks were found to have an increase in CO₂ efflux from *ca.* 634 to 951 mg CO₂ m⁻² h⁻¹ when the

temperature of the peat increased from 24 to 28 °C. Hollows produced relatively lower CO₂ efflux with an increase of 317 to 792 mg CO₂ m⁻² h⁻¹. That CO₂ efflux was more than doubled in hollows over a small temperature range of just 4 °C indicates that temperature may be of more importance in tropical peatlands than is currently thought.

This has important implications for the C balance of tropical peatlands in relation to the predicted increases in temperature in response to global climate change (Meehl *et al.*, 2007).

2.2.3 The dominant surface vegetation

2.2.3.1 Root respiration

The rooting systems of the surface vegetation can influence CO₂ and CH₄ production within the peat. There are several processes by which this occurs, one such process is the contribution from the roots (autotrophic respiration) to the CO₂ emissions from the peat surface (also contributing to total CO₂ emissions is heterotrophic respiration from organisms within the peat). This has been documented in boreal, temperate and tropical locations and estimates of the extent of root contribution are *ca.* 50 %. Andrews *et al.* (1999) found in a temperate system that root respiration contributed 55 % of the CO₂ efflux from the surface. Crow and Wieder (2005) found that root respiration was *ca.* 17 - 24 % of the total peat CO₂ efflux in a boreal peatland in Canada. Jauhiainen *et al.* (2005) found that variations in root respiration contributions to the peat surface efflux were due to differences in root biomass in the sampling locations, which was in turn affected by the microtopography of the site. Hummocks had greater root biomass and due to being raised above the water table produced root derived CO₂ of *ca.* 500 mg m⁻² h⁻¹. In hollows which had lower root biomass and a water table at the surface of the peat, root respiration contributed 100 mg m⁻² h⁻¹ to surface CO₂ efflux.

In tropical regions the growing season is not as distinct as at northern latitudes although during pronounced dry seasons productivity may drop.

In temperate soils Hanson *et al.* (2000) found substantial evidence that root respiration is linked to plant processes and as such respired at a greater rate during times of plant growth compared to dormancy. The contribution of root respiration to measured CO₂ emissions generally varies with plant species as rooting factors (such as, extent, density) vary with species, i.e. species with lower root biomass and density will likely contribute lower quantities of CO₂ to surface emissions relative to species with high biomass and densities, as found by Jauhiainen *et al.* (2005; outlined above). This relationship was also found by Li *et al.* (2004) in a tropical wet forest in Puerto Rico compared to a plantation. In this forest system root biomass was *ca.* 80 g m⁻² in the forest and contributed to *ca.* 70 % of the CO₂ efflux. The plantation had lower root biomass of *ca.* 59 g m⁻² and root respiration contributed less, at 56 %, than the forest system to surface CO₂ efflux.

2.2.3.2 Root release of exudates and oxygen

Rooting systems can influence both CO₂ and CH₄ production *via* the release of labile substrates (C source, mainly in the form of carbohydrates) into the peat profile. This input of substrates from roots can be utilised by peat microbes, sometimes preferentially to peat substrates due to its labile nature. Chanton *et al.* (1995) measured the ¹⁴C abundance of surface peat emissions and found that they were primarily composed of modern carbon suggesting that the microbial community was consuming recently fixed carbon in the form of root exudates rather than older carbon from litter or peat. Comparable results were found by Bellisario *et al.* (1999) in a Manitoba peat complex in Canada suggesting that root exudates are a main source of substrate for CH₄ production in northern peatlands. Root exudates are the products of photosynthesis and as such the timing and the quantities of exudates vary with vegetation species. Strom *et al.* (2005) found that the rate of exudate release was 7 times greater in *Eriophorum* sp. at 70 µmol acetate C g⁻¹ root h⁻¹ compared to *Carex rostrata* sp. and *Juncus effusus* at 10 µmol acetate C g⁻¹ root h⁻¹ and that after adjusting for oxidation of CH₄ in the surface layer CH₄ production was correlated positively with the rate of exudate release.

Plant roots can aerate the peat by the release of O₂ into the profile. When reviewing the literature on plant responses to anaerobic stress, Vartapetian and Jackson (1997) found extensive evidence supporting the transport of oxygen to peat via plant roots. This has the potential to increase the redox potential of the peat, for example, Choi *et al.* (2006) suggested an oxygen supply by plant roots of 0.85 g m⁻² d⁻¹ in a freshwater wetland in South Korea. The input of O₂ *via* the roots has the potential to aerate portions of the deeper peat that would otherwise be anoxic; this can potentially mean that CO₂ is produced throughout the rooting zone of the peat profile. Although at depths the peat material is of greater recalcitrance. Thus it is likely that microbial production of CO₂ is due to the microbial mineralisation of labile root exudates rather than decomposition of the peat material (Ekschmitt *et al.*, 2008). Conversely, whilst root exudates are thought to promote CH₄ production, the O₂ inputs are likely to suppress CH₄ due to the creation of oxic environments and increasingly positive redox potentials. For example, Watson *et al.* (1997) found the inhibition of CH₄ production in the rooting zone of plants in a Scottish peatland due to the oxygen concentration being too high at *ca.* 300 µmol dissolved oxygen concentration at the peat surface. This then decreased to 0 µmol oxygen at *ca.* 7 cm below the peat surface. Peat areas that did not have surface vegetation had a shallower oxygenated layer of 3 cm depth with oxygen concentrations of *ca.* 250 µmol at the surface and decreasing to zero by 3 cm depth. Dissolved CH₄ concentrations steadily increased with increasing distance below the profile and were greater in peat with surface vegetation (*ca.* 110 µmol at 20 cm depth) compared to non vegetated peats (*ca.* 90 µmol at 20 cm depth).

There is very little data on tropical plants and how they have adapted to waterlogged conditions. Examples of adaptations are; the development of extensive air spaces (termed lacunae or aerenchyma) and/or aerial roots (termed pneumatophores). Some studies, such as that by Konnerup *et al.* (2010) in studying the convective gas flow within plants of tropical wetlands, assume gas transport through the aerenchyma. To date, the

extent of the development of lacunae or aerenchyma has not been quantified in tropical species, however, data is available for temperate wetland species. For example, Smits *et al.* (1990) examined species that are commonly found in locations of highly organic sediments with a negative redox potential from the Netherlands (species examined were; *Nymphaea alba*, *Nuphar lutea* and *Nymphoides peltata*). They found that air spaces in the roots accounted for 30 - 60 % of the root. Thomas *et al.* (1996) found evidence for variation between species in Scotland when comparing *Eriophorum angustifolium* and *Carex echinata* air space percentage in the roots, which were *ca.* 12 % and 31 % air spaces respectively. These adaptations are developed in order to facilitate O₂ supply, in some species the air spaces can potentially account for the majority of the internal rooting system, for example, Kutzback *et al.*, 2004 found that the complete root cortex parenchyma formed a large aerenchyma in *Carex aquatilis* plants.

2.2.3.3 Dead root litter deposits

Dead roots can provide inputs of fresh organic material at various depths within the profile dependent on species. For example, in a freshwater riparian wetland in South Korea Choi *et al.* (2009) found that the organic matter content (over depths of 0 - 20 cm) in plots that had surface vegetation was *ca.* 10 - 30 % of the sediment, whereas non-vegetated plots had < 10 % organic matter. This is thought to be due to a combination of root exudates and fresh litter inputs (in the form of dead root material) in the rooting zone, which also influenced the microbial activity and biomass.

Dead roots have the potential to contribute substantially to peat C stores as they are deposited at depths within the peat profile, for example, Moore *et al.* (2002) estimated that the contribution of the dead roots of vascular plants to the C content of the peat was *ca.* 161 - 176 g C m⁻² y⁻¹. Dead roots that are deposited below the water table are potentially under anaerobic conditions, and as such the decomposition rate is likely to be slower. In addition to this it is likely that plant species with a greater ratio of coarse roots to fine roots will have a greater potential to contribute to

the overall C storage of the system as the coarser roots are composed of less labile material than fine roots and decompose more slowly (Chimner *et al.*, 2005). Over a 36 week period in a tropical forested peatland in Micronesia Chimner and Ewel (2004) conducted a litter bag experiment using air-dried leaves and fine roots buried at 5 cm depth in the peat. They found that root biomass litter decreased by *ca.* 30 % in comparison to plant leaves that lost *ca.* 90 % of organic matter over the same time period. This was also seen in boreal and temperate peatlands, although the rate of decomposition was slower. For example, Thormann *et al.* (2000) found that after 24 months in a peatland in Alberta, Canada, root mass loss was *ca.* 20 % from roots and *ca.* 45 % from leaves. Gill and Jackson (2000) found that the greatest root turnover occurred in tropical wetlands at *ca.* 70 % compared to temperate wetlands at *ca.* 55 % and boreal at *ca.* 45 %.

2.2.3.4 Above ground plant biomass influences

The above ground portion of the surface vegetation influences the production of gases from the peat in three ways. Firstly, the vegetation provides a source of fresh litter inputs to the peat surface. Updegraff *et al.* (1995) found that the C and N mineralisation rates of the litter were correlated with the labile fraction available to the microbial community and were negatively correlated to the recalcitrant fraction. Secondly, the vegetation produces photoassimilates. Chanton *et al.* (1995) found that the majority of the surface CH₄ was sourced from modern carbon sources most likely from the root exudation of photoassimilates. The third impact of the above ground vegetation on gas fluxes is as an alternative pathway for CH₄ emissions.

2.2.3.4.1 Fresh litter inputs

The quality of fresh litter inputs to the peat surface may affect decomposition rates as litter from different plant species varies in its composition and decomposability. Thus, litter containing a greater proportion of easily degradable material may increase the rate of decomposition, compared to species containing more recalcitrant material. Aerts *et al.* (2003) found that grassland species with a higher lignin

concentration (52 mg g^{-1} peat) had a greater CO_2 flux per gram of litter ($0.06 \text{ mg CO}_2 \text{ g}^{-1}$ dry weight of litter) compared to grasses with a lower lignin concentration (34 mg g^{-1} ; $0.02 \text{ mg CO}_2 \text{ g}^{-1}$ dry weight of litter). This was also seen by Moore *et al.* (2007) who found that a *Sphagnum* species had a lignin content of ca. 20 - 25 % and decomposed at a rate that was lower than a *Carex* species with a lignin content of 10 - 14 %. In a review of literature Jonasson *et al.* (1999) found that several studies indicated a close association of the composition of the litter (i.e. the ratio of labile:non-labile C) and the slowest mass loss was found in litters with a high lignin and low cellulose composition. The quality of litter affects the decomposition rate and is often related to the C and nutrient status of the litter in combination with the composition in terms of the fractions (labile, semi-labile and recalcitrant). For example, Aerts *et al.* (2003) found a correlation of the lignin:Phosphorus ratio with the decomposition rate of litter. A grass with a ratio of 26 decomposed at a faster rate than a grass with a ratio of 39. Therefore litter with a high ratio of cellulose to lignin is classified as high quality litter, whilst litter with a low cellulose to lignin ratio is classified as poor quality litter (Bubier *et al.*, 2007; Reiche *et al.*, 2010). This is seen within the peat profile, with typically greater labile carbon in the surface layer and increasing recalcitrance with depth. Reiche *et al.* (2010) found in an acidic fen peatland in Germany that a peat quality index, based on the labile C component of the litter, decreased with depth. This indicated that the quantity of labile C in the profile decreased with depth. In the surface 0 - 10 cm, 38 - 44 % of the organic matter was labile carbon whilst at 30 - 40 cm depth this decreased to 23 - 35 % labile carbon.

The ratios of labile C:N, C:P and N:P of the litter are important in terms of potential limitation of the microbial activity due to C and/or nutrient limitations. Litter that has low - mid ratios of C:N and/or C:P is linked to higher rates of decomposition due to the availability of sufficient C substrates and nutrients for the microbial communities. Debusk and Reddy (2005), found in the Florida Everglades, that the initial nitrogen concentration of the litter accounted for 48 % of the variability in decomposition rates. Bragazza *et al.* (2006), found that litter with a

higher C:P ratio (1975; mass loss 15 - 18 % over 1 year) decomposed slower than a litter with a lower C:P ratio (1029; mass loss 36 - 38 % over 1 year). Not all studies have found that the C:nutrient ratios are an accurate predictor of decomposition rates. Guo *et al.* (2008), found that wetland plant roots with a C:N ratio of *ca.* 37 decomposed at a slower rate than roots with a higher ratio of 40.

The timings and quantities of litter deposition can affect the decomposition process. Boreal and temperate plants often have distinct time periods in which the majority of litterfall occurs. Brinson *et al.* (1980) studied an alluvial swamp forest in North Carolina USA and found that litterfall peaked in October in both 1975 and 1976 (2.5 Mg ha⁻¹ and 1.2 Mg ha⁻¹ respectively) the majority of other months were < 0.5 Mg ha⁻¹. In a wetland in Sweden Bastviken *et al.* (2007) found variation in the organic matter content of the surface layer varied in different months of the year for *Glyceria maxima*, with 93 % in November and 77 % in August, suggesting that there is greater litter deposition in November than in August. The quantity of litterfall can also affect the rate of decomposition. In a litter bag study in a wet tropical forest in Panama, Sayer *et al.* (2006) found that the removal of the litterfall layer from the surface decreased the rate of decomposition of litterbags to 0.09 % d⁻¹ compared to 0.22 % d⁻¹ in the control plots (no litterfall removal) and 0.25 % d⁻¹ in the plots with litter added. The removal of litter decreases the substrate available to the microbial community and therefore decreases the rate of microbial decomposition.

In tropical peatlands there are no distinct seasons and no distinct timing of litterfall. However it is likely that there is increased litter deposition during the 'wet' season as there is an increased occurrence of rainfall and tropical storm events which can cause damage to plants and therefore increased litter deposition. Ostertag *et al.* (2003) found that litter deposited due to hurricane George was equivalent to 55 - 93 % of the total annual litterfall for the region. Eusse and Aide (1999) studied a tropical wetland in Puerto Rico and found increased litter deposition during storm events of *ca.* 9 g m⁻² d⁻¹ of litter, compared to typically < 4 g m⁻² d⁻¹

under calm conditions. Therefore areas with increased occurrence of storm events is likely to also have increased litter deposition to the peat surface.

Some plant species are known to be adapted to low nutrient availability by the reabsorption of nutrients before senescence. Feller *et al.* (1999) studied a Mangrove forest in Belize and found that typical phosphorus reabsorption was *ca.* 70 % and nitrogen *ca.* 45 %. When the soil was fertilised with nitrogen the phosphorus reabsorption did not change but the nitrogen reabsorption decreased to *ca.* 40 %. When the soil was fertilised with phosphorus the phosphorus reabsorption in the leaves decreased to *ca.* 50 % and the nitrogen reabsorption increased to *ca.* 70 %. This suggests that the inputs of the litter of some species to the surface is affected by the nutrient status of the soil that the individual plant is growing upon. A lower nutrient input to the soil could potentially cause nutrient depletion within the soil, for example, Sayer *et al.* (2006) found that when there was increased litter available the nutrient accumulation rates of nitrogen were 3.22 mg g⁻¹ and 0.21 mg g⁻¹ phosphorus. When the nutrient availability decreased through litter removal, the accumulation rates of the nutrients decreased to 1.39 mg g⁻¹ nitrogen and 0.06 mg g⁻¹ phosphorus. This infers a faster release of nutrients from litter deposits when nutrients are limiting. This would then further decrease the nutrient availability to microbial communities as input would be low and demand high, therefore there would be lower rates of decomposition and gas production (Rejmankova, 2001; Sayer, 2006).

2.2.3.4.2 Photoassimilates

Photoassimilates, a product of photosynthesis, are released into the peat *via* the roots (See section 1.2.3.2). The quantities and timings of photoassimilate release to peat are affected by the vegetation species and the rate of photosynthesis.

The timing of photoassimilate release is influenced by the transport time from the location of production (mainly in the leaves) to the location of release (the roots); this is commonly known as the lag time. A literature review by Kuzyakov and Gavrichkova (2010) found that phloem transport

rates of photoassimilates could range from 0.2 - 2 m h⁻¹ but typically fall between 0.5 - 1.0 m h⁻¹. It was also found that the lag time is affected by the distance that photoassimilates are to be transported rather than the method of transport, as grasses were found to release recently produced photoassimilates within minutes whereas tree transport could take days. In a forest in Northern Sweden, Ekblad and Hogberg (2001) measured the ¹³C abundance of surface effluxes and found that the C was fixed in the source compound between 1 - 4 days prior to surface emission. Therefore they suggested that the lag-time is 1 - 4 days in the trees of 20 - 25 m height in this system.

This has implications for the timing of labile C substrate release to the peat and therefore can effect the timing of increased gas production within the profile. This effect and the link to photosynthesis has been shown in several diurnal studies including Thomas *et al.* (1996) who found that the surface efflux rates during darkness were *ca.* 0.8 mg CH₄ m⁻² h⁻¹ and *ca.* 1.4 mg CH₄ m⁻² h⁻¹ during periods of light (laboratory manipulations). Tang *et al.* (2005) found that 7 - 12 h after the photosynthesis rate increased there was a corresponding increase in soil respiration. This is suggested to be the lag time of the vegetation of the oak-grass savanna in the Sierra Nevada, USA. Hirano *et al.* (2009) studied tropical peatlands in Kalimantan Indonesia and found that diurnal variation in CO₂ flux was linked to the circadian rhythm of root respiration, with a peak flux at 1100 h of *ca.* 792 - 950 mg m⁻² h⁻¹ and a low flux overnight of 317 - 457 mg m⁻² h⁻¹. Variation in solar radiation (hence photosynthetic active radiation (PAR)) received on an annual scale is likely to have greater impacts in boreal and temperate peatlands, as in tropical regions the duration of daylight hours and therefore solar radiation, varies less due to more consistent daylight hours and negligible seasonality (Chimner, 2004).

2.2.3.4.3 Vegetation as an alternate CH₄ release pathway

Several studies have shown that measurement of CH₄ emission from the surface of the peat may be a considerable under estimate of the actual CH₄ production of the peat due to the release of CH₄ *via* other pathways

(Whiting and Chanton, 1993; Watson *et al.*, 1997; Kutzbach *et al.*, 2004; Ding *et al.*, 2005). The predominant alternate pathway is *via* uptake by the roots and release from the stomata of vegetation. If CH₄ is released in this manner then it avoids passing through the potentially oxygenated surface layer and thus avoids potential oxidation to CO₂ by methanotrophic bacteria (Inubushi *et al.*, 2005). Kutzbach *et al.* (2004) studied North Siberian tundra and found that the estimate of CH₄ efflux that was released *via* the vegetation accounted for *ca.* 37 - 102 % of the total CH₄ release (which was in the range of 0.79 - 1.96 mg CH₄ m⁻² h⁻¹). Ding *et al.*, (2005) in a freshwater wetland marsh in China also found substantial plant releases of CH₄ accounting for *ca.* 73 - 86 % of the total CH₄ flux. CH₄ efflux was measured as 14 - 39 mg m⁻² h⁻¹ including vegetation efflux, and 3 - 18 mg m⁻² h⁻¹ when vegetation effluxes were excluded. It can be seen that the efflux of CH₄ *via* the vegetation may be substantially greater than the flux from the peat surface.

2.2.4 Microbial communities

Increased decomposition occurs when microbial communities increase their activity and rate of litter consumption. The activity of microbial communities is usually inferred from the production of extracellular enzymes.

Fresh litter inputs can stimulate the production of extracellular enzymes due to the increased substrate availability. For example, when comparing vegetated and non-vegetated plots in a freshwater wetland in China, Choi *et al.* (2009) found increased enzyme activities in the vegetated plots. Phosphatase (involved in phosphorus utilisation) had an activity rate of 12 - 19 µmol g⁻¹ min compared to non-vegetated plots with an activity rate of 4 - 12 µmol g⁻¹ min. The activity of β-glucosidase (involved in carbon substrate utilisation) was also greater in vegetated plots at 16 - 27 µmol g⁻¹ min compared to 1 - 6 µmol g⁻¹ min in non-vegetated plots. This demonstrates that microbial activity is limited by the available substrate

pool. Enzyme activity in wetlands is generally greatest in the surface layer, where fresh litter inputs are received, and decreases with depth. Jackson *et al.* (2009) studied a tropical Malaysian peatland and found that enzyme activities were greatest at the surface (0 cm) for 5 of the 6 enzymes measured, at 4 - 20 times the activity seen at 10 cm depth. Peroxidase activity was the only exception, with similar activities through depths 0 - 50 cm.

The availability of O₂ also varies within wetland profiles, typically being lower at depth, suggesting the possibility of greater aerobic decomposition rates in the surface horizons compared to greater depths (Wright, 2001; Jackson, 2009). For example, phenol oxidase, which produces enzymes that degrade recalcitrant materials such as lignin, requires O₂. Freeman *et al.* (2004) in a Welsh peat mire showed that the effect of O₂ availability on phenol oxidase influenced the activities of other enzymes which are not themselves directly affected by O₂ supplies. Phenol oxidase activity was found to be *ca.* 3300 µmol produced per min⁻¹ g⁻¹ peat under aerobic conditions which subsequently decreased to *ca.* 600 µmol produced per min⁻¹ g⁻¹ peat under anaerobic conditions. This group of enzymes is known as hydrolases (β-glucosidase, phosphatase, sulphatase, xylosidase and chitinase; Freeman, 2004; Jackson, 2009). Decreased phenol oxidase activity generally leads to accumulation of phenolic (humic) acid, thereby inhibiting the activity of hydrolase enzymes. This observation demonstrates that specific enzymes may influence the activity of others and suggests that changing environmental conditions may have either direct or indirect effects on enzyme activity.

2.3 Future peatland carbon dioxide and methane fluxes

Climatic shifts can affect the accumulation and degradation of carbon stored in peatlands. As discussed in section 2.1.3.1, historical periods of accumulation and degradation have been reported in peatlands the world over. Due to the current predictions for comparatively rapid changes in climate it is necessary to understand the processes leading to CO₂ and CH₄ fluxes in peatlands, to enable accurate predictions of future emission

2.3.1 Climate change predictions and gas fluxes

The current climate change predictions for Central America are; An increase in the mean temperature, by 2080 temperature changes are predicted to be +1.0 - +5.0 °C during the dry seasons and +1.3 - +6.6 °C during the wet season (IPCC 4AR, 2007). A decrease in the annual rainfall, by 2080 rainfall predictions during the dry season are -20 - +8 % and during the wet season, -30 - +5 % (IPCC 4AR, 2007).

In relation to Panama future climate change predictions typically agree that the area will become warmer and drier, the potential affect of this climate change in terms of other locations were described by both Giorgi (2006) and Baettig *et al.* (2007) using a modelling approach, both identified Central America as a region that would experience one of the strongest climate changes across tropical area in America, parts of Africa and Indonesia.

Some studies focused on quantifying the magnitude of temperature and rainfall changes, some predictions for Central America include modelled scenarios by Hulme and Viner (1998) who estimate a temperature increase of ≈ 2 °C and a rainfall decrease of -1 mm d^{-1} by 2060. A more recent model study by Solomon *et al.* (2008) predicted a 6 % decrease in rainfall for each Kelvin degree increase in temperature during the dry season.

The predicted climate change in Central America would be likely to cause lower water tables and increased peat temperatures. The potential effects of this is that peatlands in this region may become substantial sources of CO₂ as there is increasing peat aeration under WT drawdown. Concurrently there is likely to be a decrease in CH₄ fluxes and potentially the peatlands may act as a sink of CH₄ *via* surface uptake.

If in Central America rainfall decreases significantly the WT drawdown is likely to increase beyond the maximum drawdown seen currently, particularly in ombrotrophic systems. Subsequently, vegetation

communities that are adapted to frequently flooded conditions may suffer water stress, reducing the NPP of the system and also decreasing decomposition rates (and therefore heterotrophic respiration), thereby suppressing CO₂ productions in the surface layers above the WT.

2.3.2 Future land-use changes

As described in section 2.1.3.3 land-use change can potentially have a significant impact on the release of carbon from peat stores. Many peatland areas are already degraded, mainly due to anthropogenic impacts. For example, Miettinen and Liew (2010) using satellite imaging from 2005 - 2008 that covered 83 % of the peatlands in Sumatra and Kalimantan, assessed the current status of these peatlands in terms of degradation. They found a total peatland area of 4.4 Mha occupied by peatswamp forest. Of this < 11 % was determined to show either minor or no signs of anthropogenic activity. The vast majority of the identified peat swamp forest was either moderately or heavily degraded. This has implications for the future of peatlands, with such a substantial area already classed as degraded, the risk of fires as well as future degradation is high. Hooijer *et al.* (2010) when analysing available data, also found substantial degradation of peatlands in SE Asia, with 47 % (\approx 6.3 Mha) of peatlands deforested by 2006.

Patterns of peatland degradation are often explained by their ease of access, with the most degraded peatlands in area of high populations (Miettinen and Liew, 2010). With the predicted future increases in human populations it is likely that more land will be needed for processes such as food production, which may threaten the relatively small percentage of remaining undisturbed peatlands.

The degradation of SE Asian peatlands has been investigated in the literature, however other areas of the tropics have not been as exhaustively quantified and as such it is difficult to determine the current degradation of tropical peatland. What is known is that drained and deforested peatlands are susceptible to fires (Miettinen and Liew, 2010;

Page *et al.*, 2011) with climate change predictions for central America being towards warmer and drier conditions, the threat of fires, such as those seen in Indonesia (Page *et al.*, 2004) becomes of increasing concern.

Future predictions of gas fluxes from degraded peatlands is difficult to quantify, what is likely is that CH₄ flux would decrease and CO₂ flux increase, due to drainage. However, CO₂ fluxes will potentially peak and then decrease, as the peat deposits decrease in extent. For example, Hooijer *et al.* (2010) estimate that the peak of CO₂ emissions from peatlands of SE Asia will occur in 2015 at $\approx 745 \text{ Mt yr}^{-1} \text{ CO}_2$ before decreasing.

2.4 Study aims

Studies of tropical peatlands are important due to the relative scarcity of information compared to boreal and temperate peatlands concerning the factors which control decomposition and carbon storage. Much of the existing data on tropical peatlands is focused on the extensive peat deposits in SE Asia. Neotropical peatlands are estimated to store c. 12.5 Gt C (Page *et al.*, 2011) but this is likely to be an underestimate as new areas of peatland are regularly reported within this region (e.g. Lahteenoja *et al.*, 2009; Vegas-Vilarrubus *et al.*, 2010). Furthermore, their undisturbed nature makes them valuable resources for developing a mechanistic understanding of the processes governing C storage and potential future release of C. The objectives of this study were to attempt to:

- i) characterise the spatial and temporal variation in CO₂ and CH₄ fluxes within a domed ombrotrophic Neotropical peatland
- ii) determine the relative importance of nutrient availability, temperature and fluctuations in the water table in controlling decomposition and CO₂ and CH₄ fluxes in this system
- iii) assess the contribution of deeper peat layers to surface CO₂ and CH₄ fluxes

- iv) provide information required to improve the reliability of predictions of future C storage and release from tropical peatlands.

Six hypotheses were formulated to achieve these aims, these were:

- i) CO₂ fluxes will be higher during the dry season compared to the wet season. CH₄ fluxes will be lower during the dry season compared to the wet season due to variations in environmental conditions.
- ii) CO₂ and CH₄ fluxes will vary on a diurnal basis, due to variations in peat and vegetation processes.
- iii) CO₂ and CH₄ fluxes will vary between sites of differing dominant vegetation, due to differences in the peat chemical and physical properties linked to the surface vegetation.
- iv) CO₂ and CH₄ fluxes will vary within sites of the same dominant vegetation in response to microtopography variations.
- v) CO₂ and CH₄ fluxes from the peat will decrease with increasing depth from the peat surface in response to the increasingly recalcitrant peat material and corresponding decrease in microbial activity with depth.
- vi) The quality of litter inputs and the microbial activity influences CO₂ and CH₄ fluxes, with an increase in microbial activity (and hence increased flux) corresponding to higher quality litter material.

The following table details which chapters these hypotheses will be investigated in

Chapter Number	Chapter Title	Hypotheses tested
4	Influence of carbon and nutrient concentrations of leaf litter and peat on carbon dioxide and methane fluxes	i, iii, iv
5	Temporal variation in CO ₂ and CH ₄ fluxes on an annual and diurnal basis	i, iii, v
6	Variation in gas fluxes from 0 - 2 m depth within the peat profile	iii, vi
7	Nutrient cycling at three sites in the San San Pond Sak wetland, Panama	iii, vi

Chapter 3 Materials and methods

3.1 Site description

The San San Pond Sak peatland is a 164 km² mosaic of freshwater and marine-influenced wetlands in Bocas del Toro Province on the Caribbean coast of western Panama (Cohen & Stack, 1996). Recognised internationally as a site of special scientific interest (Ramsar site #611), it includes the significant 80 km² Changuinola peat deposit, an ombrotrophic domed peatland to the south east of the Changuinola River. As an undisturbed site of several type of vegetation, San San Pond Sak provides a good exemplar location of peatlands in Panama to enable quantification of gas fluxes from peat in Panama.

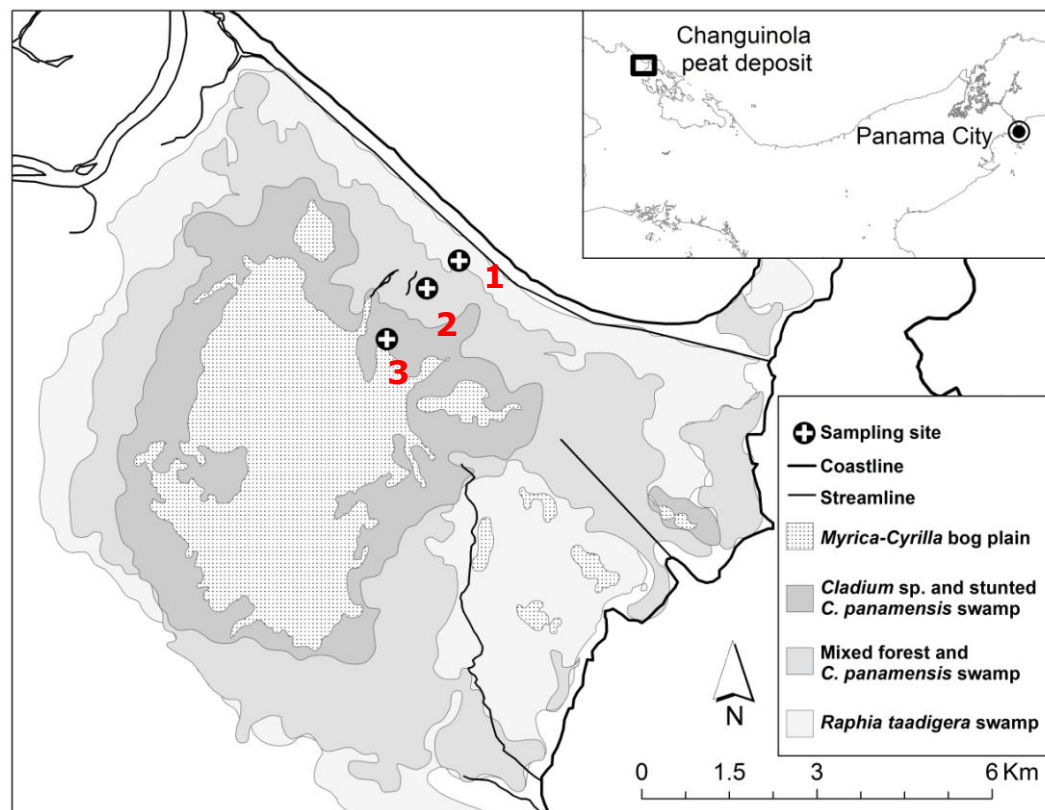


Figure 3.1. The location of the Changuinola peat deposit and sample sites locations 1-3.

The oldest deposits in the Changuinola peatland are estimated to have been formed 4000–4500 years ago and are >8 m deep in the central

areas, peat at the edges of the peatland is *ca.* 2 m deep (Phillips *et al.*, 1997). The vegetation communities which formed the peat have shifted spatially over time, meaning that carbon inputs and environmental conditions at specific locations have differed greatly (Phillips *et al.*, 1997). The texture of the peat varies between the interior, where it is predominantly coarse to a depth of 2-4 m and dominated by roots in the surface layers, to the edges where the peat has a fine texture throughout the profile (Phillips *et al.*, 1997), indicating greater decomposition and/or differences in the source of litter.

Seven distinct phasic plant communities cover the peatland in approximately concentric rings (Phillips *et al.*, 1997). Starting from the periphery, these communities have been designated as (i) *Rhizophora mangle* mangrove swamp, (ii) mixed back mangrove swamp, (iii) *Raphia taedigera* palm swamp, (iv) mixed forest swamp, (v) *Camptosperma panamensis* forest swamp, (vi) sawgrass/stunted forest swamp and (vii) *Myrica-Cyrilla* bog-plain. Nutrient levels in the peat and plant tissues vary greatly between vegetation communities and are generally low in the interior and higher towards the edge of the peatland (Troxler, 2007; Sjögersten *et al.*, 2010). Previous work has shown that the low nutrient content in the interior is reflected by reduced microbial activity, with lower microbial biomass C:N and C:P ratios and increased activity of extracellular enzymes involved in nutrient acquisition (Sjögersten *et al.*, 2010). Furthermore, *in situ* CO₂ and CH₄ fluxes did not appear to reflect nutrient availability, while drained surface peat samples exhibited lower CO₂ production in material from the interior than sites closer to the edge of the peatland (Sjögersten *et al.*, 2010).

Meteorological data from the met station at the Smithsonian research facility on the nearby town of Bocas del Toro, Isla Colon, *ca.* 10 km from the peatland, was utilised to determine the climatic conditions of the area. This was the closest available meteorological data collection point and as such should provide a good indication of the conditions found in San San Pond Sak. This area has a mean annual temperature of 27 °C with low intra-annual variability and a mean annual precipitation of 3209 mm

between 1992 and 2001 (Estadística Panameña, 2001). Rainfall is continuous throughout the year with no pronounced dry season, although there are two distinct periods of lower rainfall (February–April and September–October). The water table is generally at the surface of the peatland throughout the year, with no distinct period of draw down. Mean peat temperature 10 cm below the surface is *ca.* 25 °C and shows little intra-annual variation (Sjögersten *et al.*, 2010).

Three sample locations were selected that represented the three major species of dominant vegetation across the transect, they were 1) *Raphia taedigera* palm swamp, 2) *Camptosperma panamensis* forest swamp and 3) sawgrass/stunted forest swamp (Fig. 3.1)

3.1.1 *Raphia taedigera* palm swamp

The *Raphia taedigera* (*R. taedigera*) palm swamps had little to no understory vegetation. *R. taedigera* is formed of clusters of individual stems with large leaves *ca.* 15 m plus in length (Fig. 3.2; Phillips *et al.*, 1997).

Stem density was estimated at 106 stems ha⁻¹ with a basal area of 103 m² ha⁻¹ (Sjögersten *et al.*, 2010). The tree species Shannon diversity index was 1.13 (Sjögersten *et al.*, 2010). The canopy cover was estimated at *ca.* 80 - 90 % (Fig. 3.3). Litterfall was extensive and leaf litter covered the majority of the peat surface (Fig. 3.4).



Figure 3.2 *R. taedigera* palm species, stem formation



Figure 3.3 *R. taedigera* canopy cover taken at *ca.* 70° relative to the peat surface.



Figure 3.4 *R. taedigera* litterfall on the peat surface detailing typical litter distribution

3.1.2 *Campnosperma panamensis* forest swamp

The *Campnosperma panamensis* forest swamp had a mixed understory vegetation that was primarily formed of a sawgrass species (genus not identified; Fig.3.5). The tree basal area was $26 \text{ m}^2 \text{ ha}^{-1}$ and the stem density $212 \text{ stems ha}^{-1}$ (Sjögersten *et al.*, 2010). Tree trunks were *ca.* 20 - 30 cm diameter (Fig. 3.6). The Shannon index of diversity for tree species was 1.53 (Sjögersten *et al.*, 2010). The canopy cover was estimated at 90 - 95 % (Fig. 3.7). Trunks were bare of branches to *ca.* 10 - 15 m height (Phillips *et al.*, 1997) and were *ca.* 20 - 25 m in total height. Litterfall formed a layer of decomposing leaves across the site except on the root mounds at the base of *C. panamensis* trunks.



Figure 3.5 *Camphosperma panamensis* site showing sawgrass understory vegetation



Figure 3.6 *Camphosperma panamensis* typical trunks



Figure 3.7 Canopy cover at the *Camptosperma panamensis* site

3.1.3 Sawgrass/stunted forest swamp

Cyperus species were identified throughout the sawgrass/stunted forest swamp (Philips *et al.*, 1997) and as such this site is henceforth referred to as *Cyperus* sp. site. Individual plants were closely spaced (Fig. 3.8) with stunted *Camptosperma panamensis* trees interspersed (Fig. 3.9). The tree basal area was low at 5 m² ha⁻¹ with a high stem density at 423 stems ha⁻¹, the Shannon index of tree diversity was higher than at the other two sites at 1.83 (Sjögersten *et al.*, 2010).

3.2 General Materials and Methods

This section contains materials and methods that were common throughout the study. Specific protocols are found in the materials and methods section of the subsequent results chapter.



Figure 3.8 *Cyperus* sp. site. Note that the clear standing water is the trail cut through the site



Figure 3.9 *Cyperus* sp. site with a stunted tree corpse in the background. Note the clear standing water is the trail cut through the site

3.2.1 Peat surface flux

3.2.1.1 In situ sampling

In situ surface peat fluxes were sampled using one of two headspaces, hereafter referred to as headspace A and headspace B. Headspace A was 810 cm² and *ca.* 10 cm high. The total volume was 7.8 dm³. To ensure a good seal with the peat surface the headspace had a flexible plastic 'skirt' attached, which was then held down on the surface with a metal chain. Headspace B was 10 cm in height and had a volume of 0.45 dm³. To ensure a good seal with the peat surface, headspace B was gently pressed into the peat surface to *ca.* 0.3 cm depth. These methods were chosen due to the nature of the field site sampled, headspace A was designed to be able to be left in location between sampling events to minimize the amount of equipment carried to and from sample locations. After a year of field sampling headspace A began degraded due to exposure so headspace B was chosen to provide a lightweight headspace that could be easily transported to and from sample sites.

Prior to sampling, the vegetation was carefully removed from the plots where necessary (mainly at the interior *Cyperus* site) by severing it at ground level, whilst roots and pneumatophores were left in place; removal of the above-ground vegetation may have resulted in underestimation of CH₄ and CO₂ emissions as plant emissions of gases was not quantified in this study. The headspace was placed on the peat surface and sealed as described above. Thereafter 25 ml samples of air were collected *via* a Suba-Seal[®] using a syringe 0, 2, 10 and 20 min after fitting headspace A and at 0 and 10 min for Headspace B; the sampling time was adjusted to account for the smaller head space (Yao *et al.*, 2009). Samples were then transferred to 12 ml vacuumed exetainers (Labco, High Wycombe, UK). All samples were shipped to the University of Nottingham for CO₂ and CH₄ analysis. As an over-pressure was injected into the vials, it was easy to detect any loss of sample during transport; samples were discarded when this occurred (less than 2 %). The samples from each head space were checked for linearity prior to the gas flux calculations to ensure accurate calculation of gas emissions.

3.2.1.2 Peat surface flux analysis

CO₂ and CH₄ concentrations were analysed simultaneously using a Gas Chromatograph (GC-2014, Shimadzu, Milton Keynes, UK) fitted with a flame ionising detector for CH₄ detection and a thermal conductivity detector for CO₂ detection. The GC was fitted with a 1 ml sample loop and a molecular sieve column. The column temperature was 40 °C and the carrier gas was H₂.

3.2.1.3 Ex situ peat surface flux

Ex situ surface CO₂ flux was measured using a portable infra-red gas analyser (IRGA, model EGM - 1 with a SPY - 1 soil cuvette). For these measurements the peat material was placed in a container within the cuvette and sealed.

3.2.2 Determination of peat characteristics

For all peat samples that were collected in the field, they were stored at the Smithsonian Institute on Isla Colon, Bocas del Toro at 4 °C for no more than 2 days before processing (detailed below). 25 ml surface water samples were collected in the field using a plastic syringe. The water samples were transferred to plastic screw-top tubes and were stored at 4 °C at the Smithsonian for no more than 4 hours before each sample was filtered using a 0.22 µm filter and placed in a clean plastic screw-top tube. Samples were then frozen during storage and transport.

3.2.2.1 Initial processing of peat samples following collection

These protocols were carried out at the Smithsonian prior to transport of samples to the University of Nottingham.

Redox potential was determined using a KDCMPtB11 redox probe (Thermo Electron Corporation, Altrincham, UK). The probe was carefully inserted *ca.* 3 cm into the peat and allowed to stabilise for 5 min before completing the measurement. Living roots were separated by their colour and condition and all recovered material was rinsed in deionised water and air-dried. Moisture content was calculated for fresh sub-samples by

gravimetric loss after 70 h at 70 °C (the longer than is usual time span was due to the limitations of equipment available at the field station), while pH was determined using a 2:1 fresh peat:deionised water ratio and glass electrode. Bulk density was determined by taking a sub-sample of each peat sample in the laboratory, recording the fresh weight of each sample and calculating its dry weight using a wet-dry weight conversion factor based on the moisture content. Bulk density was calculated by dividing the dry peat weight (determined by drying at 70 °C for 70 h) by the sample volume (used for peat core samples only). Organic matter content was estimated from loss on ignition (LOI) after ashing 250 mg of ground air-dried material at 550 °C for 4 h in borosilicate scintillation vials. Porewater samples were collected using 10 cm long Rhizon samplers constructed from hydrophilic porous polymer with a pore diameter of ca. 0.1 µm to exclude soil particles (Rhizosphere Research Products, Wageningen, The Netherlands). Samples were frozen during storage and transport.

When all initial peat processing had been performed the remaining peat material was air dried at 26 °C, then placed in ziploc bags and transported to the University of Nottingham.

3.2.2.2 Carbon and nutrient determination

3.2.2.2.1 Peat material

Dried peat samples were ground to a fine powder and total organic carbon and total nitrogen were analysed using a CNS total element analyser (Flash EA 1112 Series, CE Instruments Ltd, UK). Total phosphorus (TP) was analysed by ashing 0.2 g of peat sample at 550 °C for 3 h. The ashed material was weighed before being placed in a screw top tube with 20 ml of 1 M H₂SO₄ (to provide a ratio of 10 ml of acid per 0.1 g of sample) and shaken for 24 h. The solutions were allowed to settle before removing and analysing the supernatant for TP using molybdate spectroscopy (see below).

3.2.2.2.2 Water samples

Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were measured in water samples and were subsequently analysed using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). TP was measured using standard molybdate spectroscopy with an absorbance wavelength of 880 nm.

Chapter 4. Influence of carbon and nutrient concentrations of leaf litter and peat on carbon dioxide and methane fluxes

4.1 Introduction

Although greenhouse gas emissions from tropical peatlands are of global significance (Couwenberg *et al.*, 2010), the mechanisms controlling these are not fully understood. Spatial variability in carbon dioxide (CO₂) and methane (CH₄) fluxes from the surface of tropical peatlands is often high (Sjögersten *et al.*, 2010) within and among a range of vegetation communities (Jauhainen *et al.*, 2005; Melling *et al.*, 2005a, b). Several factors have been identified as important drivers of variability on various spatial scales namely: (i) the depth of the water table relative to the peat surface (Jauhainen *et al.*, 2005), (ii) dominant vegetation type (Bridgham and Richardson, 1992), and hence the quality of litter inputs and lability of the surface peat (Chanton *et al.*, 2008; Wright *et al.*, 2011), (iii) the nutrient status of the peat (Sjögersten *et al.*, 2010), (iv) and below-ground impacts of roots on the oxygenation of peat profiles (Konnerup *et al.*, 2010; Fritz *et al.*, 2011).

Microbial production of CO₂ and CH₄ utilises carbon (C), nitrogen (N) and phosphorus (P) from the litter deposited on the peat surface. The C, N and P held in litter and peat vary in lability, depending on the fraction of the litter in which they are held (Bridgham and Richardson, 2003; Cheesman *et al.*, 2010), and the degree of peat degradation (Grover and Baldock 2010; Wright *et al.*, 2011). The most labile fraction is generally water soluble and rapidly leaches from the litter, particularly if the water table (WT) is above the peat surface (Yule and Gomez, 2009; *cf.* Section 7.3.1). Greater concentrations of labile C, N and P are generally associated with high initial rates of OM loss, as this fraction is utilised by microbes or leached in drainage water (Jonasson and Shaver, 1999; Battle *et al.*, 2007). Indeed, CO₂ and CH₄ production may be greater in peat with high concentrations of dissolved organic C and N than in poorer quality peat (Bridgham and Richardson, 1992; Charman *et al.*, 1999; Chanton *et al.*, 2008). Less labile fractions held in relatively easily

degradable substrates such as cellulose are broken down by microbial extracellular enzymes (Williams and Yavitt, 2003; Choi *et al.*, 2009) and may also contribute substantially to CO₂ and CH₄ production (Wright *et al.*, 2011). Lower rates of gas production occur from the more recalcitrant litter and peat fractions from materials which are resistant to degradation such as lignin, which only degrade slowly (Jonasson and Shaver, 1999; Chimner and Ewel, 2005), particularly under anaerobic conditions where the activities of phenol oxidases and peroxidases are low (Freeman *et al.*, 1998; Sinsabaugh *et al.*, 2010). The quality of litter is affected by the source species and nutrient status of the peat. Some plant species are known to re-absorb nutrients from leaves before senescence, therefore decreasing nutrient inputs to the peat (Feller *et al.*, 1999).

The level of the water table (relative to the surface of the peat) influences the breakdown of litter and peat material (Battle *et al.*, 2007; Makiranta *et al.*, 2009). When the water table is high, oxygen supplies are reduced, decreasing the activity of aerobic heterotrophic microbes. Concurrently, the activity of anaerobic microbes increases but the rate of decomposition is substantially slower than that of aerobic degradation (Melling *et al.*, 2005a, b). In tropical peatlands this relationship between gas production and water table depth increases CO₂ release when the water table is low and CH₄ production when the water table is high, (Furukawa *et al.*, 2005; Hadi *et al.*, 2005; Hirano *et al.*, 2009; Couwenberg *et al.*, 2010). Micro-topography has been found to impact strongly on net CO₂ and CH₄ release in relation to water table drawdown, as CO₂ efflux is greater from aerated hummocks than waterlogged hollows (Schwendenmann *et al.*, 2003; Chimner, 2004; Jauhiainen *et al.*, 2005). The opposite applies when the water table falls below the peat surface to the point where the drawdown occurs to depths which cause water stress and decrease the rate of aerobic degradation (Laiho, 2006; Moore *et al.*, 2007). Indeed, Hirano *et al.* (2007) found that CO₂ release from peat increased as moisture content increased from <0.25 m³ m⁻³ to >0.35 m³ m⁻³. Plants can also strongly affect below ground O₂ concentration and hence redox potential within the peat through convective flow (Konnerup *et al.*, 2010) to a point where no net CH₄ emissions can be detected (Fritz *et al.*, 2011).

Some studies have shown that nutrient availability in peat is a key controlling factor in litter and peat decomposition (Debusk and Reddy, 2005; Battle *et al.*, 2007; Sjögersten *et al.*, 2010). The lack of a specific nutrient (typically N or P) often decreases the rate of degradation and activity of extracellular enzyme activities (Quested *et al.*, 2003; Debusk and Reddy, 2005; Sjögersten *et al.*, 2010) and application of nutrients to nutrient-limited wetlands may increase decomposition due to the increased demand for C from microbes and therefore increase CO₂ release (Bubier *et al.*, 2007; Cheesman *et al.*, 2010). Concurrently, extracellular microbial enzymes which extract previously limiting nutrients may decrease in abundance. This is often the case when peatlands are drained to provide agricultural land and subsequently receive fertiliser applications (Aerts *et al.*, 2003). Due to the significant store of recalcitrant C within peat, this has high potential to contribute to increased greenhouse gas emissions.

Temperature is known to affect the rate of litter decomposition, with higher temperatures typically linked with an increased rate of decomposition (Jonasson and Shaver, 1999; Domisch *et al.*, 2005). This effect is generally seen in temperate and boreal systems where the distinct seasons impose relatively large temperature variations (Domisch *et al.*, 2005; Makiranta *et al.*, 2009). In tropical regions there is often very little temperature variation over time (Domisch *et al.*, 2005; Hirano *et al.*, 2009; Couwenberg *et al.*, 2010) with the result that seasonal temperature variation is a relatively minor driver of CO₂ and CH₄ production under the current climate regime (Hashimoto *et al.*, 2004; Sjögersten *et al.*, 2010). This has important implications for the C balance of tropical peatlands in relation to the predicted increases in temperature (Meehl *et al.*, 2007). There may also be potential temperature affects due to land-use change, for example, the draining of peatlands and conversion to plantation often results in an increase in peat temperature due to greater exposure of the peat surface under reduced surface vegetation biomass (van der Werf *et al.*, 2008; Miettinen and Liew, 2010; Page *et al.*, 2011).

The work described in this Chapter examines the factors controlling small scale spatial variability in CO₂ and CH₄ production in a tropical peatland with a known nutrient gradient (Phillips *et al.*, 1997; Troxler, 2007; Sjogersten *et al.*, 2010) using three experiments. Firstly, gas efflux, the nutrient status of peat and surface water, and water table depth were determined *in situ* at three sites with contrasting vegetation communities and nutrient status. Secondly, the influence of vegetation type on small scale variability was investigated by measuring CO₂ and CH₄ fluxes with increasing distance from the centre of *R. taedigera* palm clumps. Thirdly, temperature and nutrient responses of the heterotrophic respiration (i.e. CO₂ production) in drained peat were assessed in an *ex situ* laboratory incubation experiment using root-free peat from all three sites.

4.2 Materials and Methods

4.2.1 *In situ* variation

A detailed survey of peat properties was carried out for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites during August and September 2009. At each site, a 10 m² grid containing nine sampling points was established (Fig. 4.1). The number of sampling locations at each site was limited by the time available for sampling at the least accessible interior site. Mean peat temperature at 10 cm depth at the time of sampling at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites was 26.4, 26.0 and 26.5 °C respectively, while mean air temperature measured 100 cm above the ground surface was 27.0, 24.0 and 33.0 °C. The water table at the time of sampling was at the peat surface, but the microtopography at each site resulted in shallow hollows being submerged in c. 5 cm of water while hummocks were c. 5 cm above the water table.

Sampling positions were located in undisturbed areas at least 10 m from the path. Surface gas fluxes were collected once between the hours of

1000 and 1300 (c. 1000 h, 1130 h and 1230 h for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites respectively) using a 384.8 cm³ headspace as described in Section 3.2.1.1. If the water table was above the peat surface, the depth of standing water was recorded and water samples were taken with a 25 ml syringe as described in Section 3.2.2.

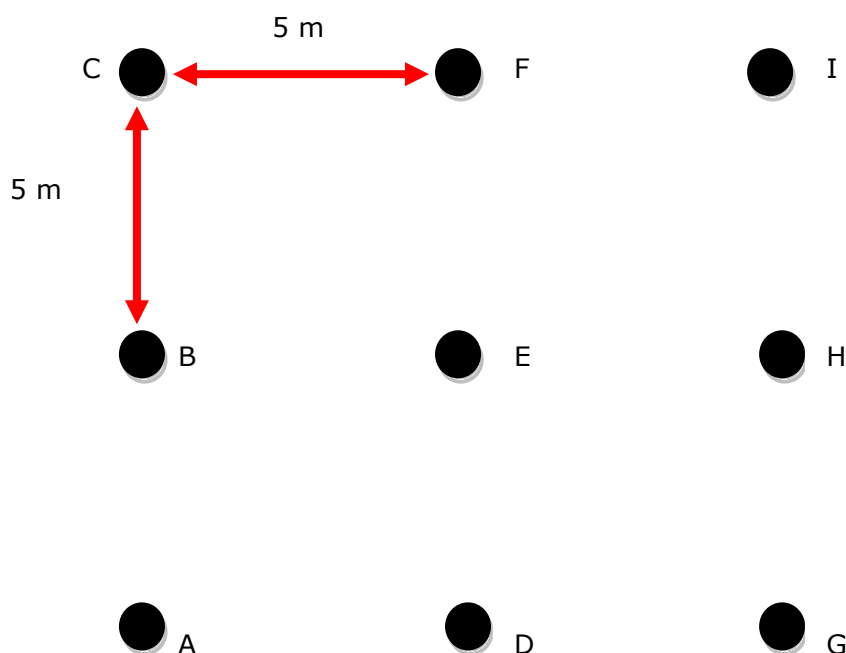


Figure 4.1. Sampling grid for the spatial surveys at the *C. panamensis* and *Cyperus* sp. sites.

The height of hummocks protruding above the water table table was recorded. If there was no standing water at the point of headspace sampling, water samples were taken from standing water within 20 cm of the headspace. If there was no water within this radius no sample was taken. Samples were filtered to remove suspended material and frozen before being transported to Nottingham for analysis of total dissolved organic C (DOC), dissolved N (DN) and dissolved P (DP) using the methods described in Section 3.4. A 10 x 10 x 10 cm sample of the surface (0–10 cm) peat directly under the headspace was collected and placed in a plastic Ziploc bag, stored at 4 °C and processed within two days of collection. Living roots were removed to avoid input of their biomass to the C and nutrient determinations of the peat before air-drying

the samples at 26 °C. The dried samples were placed in sealed plastic bags and transported to the University of Nottingham for C, N and P analysis as described in Section 3.2.2.

4.2.2 Comparison of two locations in an area dominated by *R. taedigera*

To investigate spatial variability on a wider scale and explore the influence of the dominant vegetation on surface CO₂ and CH₄ emissions, gas fluxes were measured at three distances from the centre of *R. taedigera* palm clumps at two locations referred to hereafter as Sites A and B. Site A was the original sample location used throughout the project and described in Section 3.1.1, whereas site B was located c. 500 m East of site A and the same approximate distance from the edge of the peat formation.

At each site, three *R. taedigera* palms were selected, situated c. 20 m from each other. Twelve sample plots were chosen around each tree at three distances i.e. directly next to the base of the stem and at distances

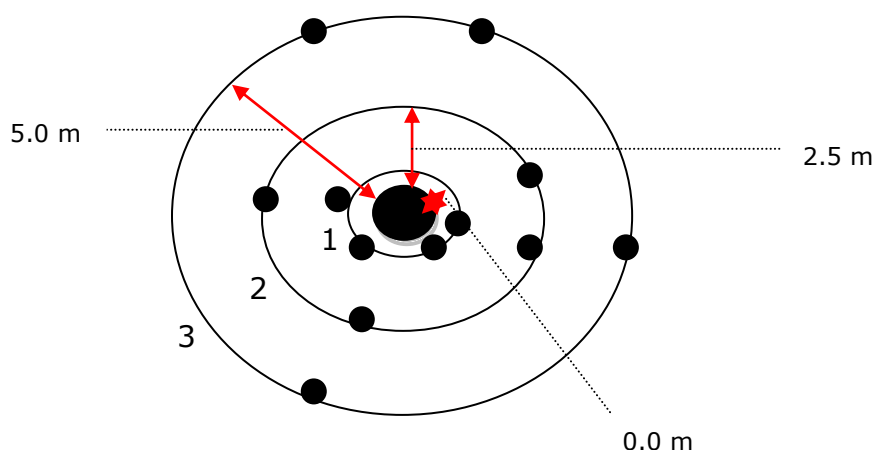


Figure 4.2. Diagram showing the distance of the rings from *R. taedigera* palms where samples were taken. The three rings are numbered 1–3 from the palm outwards with ring 3 approximately representing the outer edge of the canopy

of 2.5 and 5 m; the latter approximately represented the outer edge of the canopy and therefore included the majority of the litterfall area (Fig.

4.3). The rings are denoted as: 1) closest to the palm; 2) 2.5 m distance; and 3) 5 m from the tree.

The locations of the 12 sample plots around each tree were selected using a random number generator. Within each plot, CO₂ and CH₄ fluxes and samples for peat and surface water were collected for analysis and processed as described in Section 3.2.1 and the position of the peat surface in relation to the water table was recorded.

4.2.3 Influence of temperature and nutrient treatment on ex situ CO₂ efflux from peat samples at field capacity

To determine the effect of temperature and nutrient limitation on the decomposition of peat and CO₂ production, a series of experiments was carried out on peat collected from the three study sites used in the spatial survey described above. At all three sites, four plots were selected located at least 20 m apart. Thereafter 10 x 10 x 10 cm samples of surface peat were taken from directly beneath the headspaces, transported to the Bocas del Toro laboratory and stored at 4 °C for no more than two days prior to analysis.

Sub-samples of each peat sample (c. 10 g) were weighed and dried at 70 °C for 24 h to determine their dry weight. The remaining samples were allowed to drain overnight until field capacity was reached. Live roots were removed to avoid fresh biomass inputs and eliminate any contribution of root respiration to the CO₂ flux measurements before combining the samples to form one large composite sample for each site. This was then divided in 125 g sub-samples which were placed in circular 10 cm diameter polystyrene tubs with a depth of 4.2 cm. The samples were allowed to settle overnight at 4 °C and incubated for 4 h at 22 °C before applying seven nutrient treatments: 1) Low N, 2) Low P, 3) Low N and P, 4) High N, 5) High P, 6) High N and P and 7) control. The low and high application rates were respectively 0.01 and 0.1 mg g⁻¹ peat. Each treatment was applied to eight samples from the *R. taedigera* and *C. panamensis* sites and six samples from the *Cyperus* sp. site. Nutrient

applications were dissolved in 5 ml of deionised water and applied using a syringe as evenly as possible to the surface of the samples. The control treatment received 5 ml of deionised water.

After applying the nutrient treatments, the samples were incubated at 22 °C for 4 h before measuring CO₂ fluxes using a portable infra-red gas analyser (IRGA, model EGM-1 with a SPY-1 soil cuvette). Temperature was then increased to 27 °C and finally to 32 °C before repeating the measurements. Sub-samples of c. 20 g were frozen for later enzyme assays (*cf.* Chapter 7).

4.2.4 Data analysis

All statistical analyses were performed using Genstat version 11 (Lawes Agricultural Trust, Rothamsted Experimental Station). All CO₂ and CH₄ fluxes were tested for normality before using a Shapiro-Wilk's test to test for significance ($p < 0.05$) and visual inspection of quantile-quantile plots. If the null hypotheses were rejected the data was transformed to meet the assumptions of normality.

To test variation across sites, analysis of variance (ANOVA) tests for CO₂ and CH₄ fluxes and organic carbon, total nitrogen and phosphorus, and dissolved organic carbon, nitrogen and phosphorus as variants were performed, with site as the treatment structure. To test the influence of environmental factors on gas CO₂ and CH₄ production, linear regression analyses were performed at each site for water table, C and nutrient factors. The relationship between CO₂ and CH₄ production was tested using a linear regression with CO₂ as the response variant.

In the experiment exploring the influence of distance from the centre of trees on CO₂ and CH₄ fluxes, an ANOVA was run with site, tree, ring and their interactions as the treatment structure. Sites A and B were then tested separately with tree, ring and interactions as the treatment structure and CO₂ and CH₄ fluxes as response variants. A final ANOVA involving both sites tested for variation CO₂ and CH₄ fluxes with site, ring and their interactions as treatment structure and tree as a blocking term;

environmental variables were run as covariates to test for their influence on fluxes.

Prior to analysis of the *ex situ* temperature and nutrient manipulation of peat from the three sites, the CO₂ fluxes were expressed in terms of mg CO₂ g⁻¹ peat h⁻¹. Two separate unbalanced ANOVAs were used to test for significant effects between sites and treatments. Firstly, significant effects of 'Site', 'Temperature' and their interactions on the CO₂ flux from control peat (i.e. peat that was not amended with nutrients) were tested on an overall and individual site basis. Nutrient effects were tested on an overall and site basis using an overall unbalanced ANOVA with site, nutrient amendment and interaction as the treatment structure. Individual unbalanced ANOVAs had nutrient amendment as the treatment structure. These analyses were repeated for each temperature.

4.3 Results

4.3.1 Variation among sites differing in dominant vegetation types

CO₂ and CH₄ fluxes were both greatest at the *Cyperus* sp. site (CO₂: 445.3 ± 94.9 mg m⁻² h⁻¹, CH₄: 6.93 ± 2.27 mg m⁻² h⁻¹, Figs. 4.3 and 4.4) followed sequentially by the *C. panamensis* (CO₂: 272.3 ± 61.6 mg m⁻² h⁻¹, CH₄: 2.91 ± 1.08 mg m⁻² h⁻¹) and *R. taedigera* (CO₂: 218.9 ± 39.3 mg m⁻² h⁻¹, CH₄: 0.81 ± 0.34 mg m⁻² h⁻¹) sites.

Total C, N and P concentrations in the peat differed among sites (Fig. 4.5); C and N concentrations were greatest at the *R. taedigera* (C: 589 ± 45 mg g⁻¹, N: 28.4 ± 2.4 mg g⁻¹) site and lowest at the *Cyperus* sp. (C: 383 ± 12 mg g⁻¹, N: 21.3 ± 0.9 mg g⁻¹) site. P concentration was greatest for the *C. panamensis* (0.79 ± 0.05 mg g⁻¹) site followed successively by the *Cyperus* sp. (0.60 ± 0.06 mg g⁻¹) and *R. taedigera* (0.37 ± 0.08 mg g⁻¹) sites.

The concentrations of C, N and P in the surface water varied significantly between sites (Fig. 4.6). C concentration was greatest at the *R. taedigera*

site ($28.5 \pm 3.2 \text{ mg l}^{-1}$), where the value was over 20- and 70-fold greater than at the *C. panamensis* ($1.2 \pm 0.3 \text{ mg l}^{-1}$) and *Cyperus* sp. ($0.3 \pm 0.0 \text{ mg l}^{-1}$) sites respectively. The N concentration of the surface water at the *C. panamensis* site ($15.6 \pm 1.5 \text{ mg l}^{-1}$) was c. 2- and 6- fold greater than at the *Cyperus* sp. (6.9 mg l^{-1}) and *R. taedigera* ($2.4 \pm 0.5 \text{ mg l}^{-1}$) site, respectively. The P concentrations of the surface water at the *R. taedigera* ($0.205 \pm 0.048 \text{ mg l}^{-1}$) and *C. panamensis* ($0.185 \pm 0.049 \text{ mg l}^{-1}$) sites were comparable and much greater than at the *Cyperus* sp. ($0.003 \pm 0.000 \text{ mg l}^{-1}$) site.

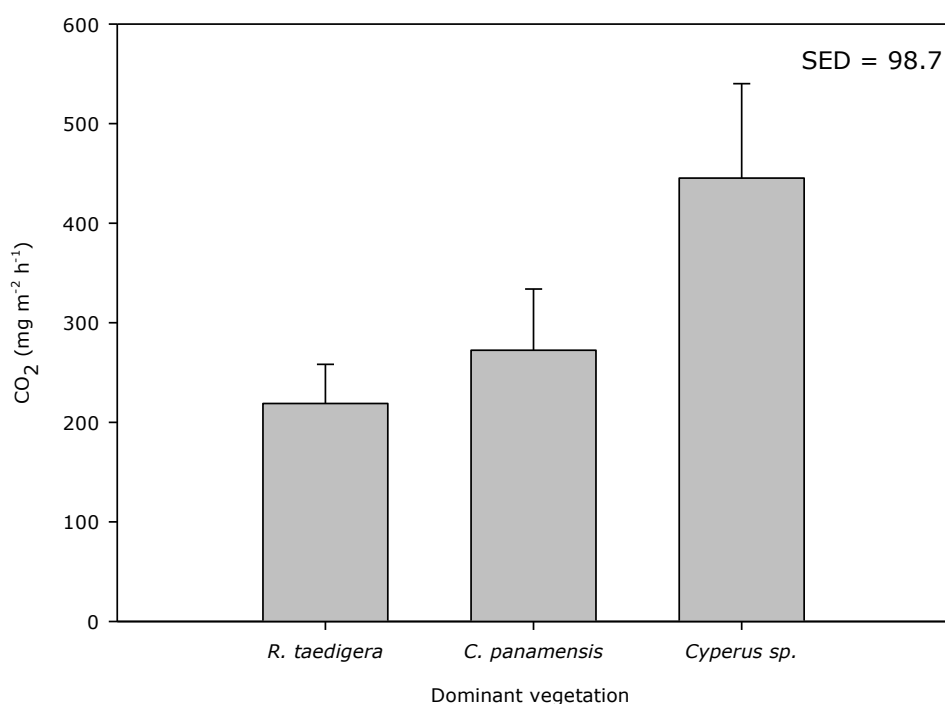


Figure 4.3. Mean CO₂ fluxes from the peat surface at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites. Single standard errors of the mean are shown (n=9 replicates). ANOVA test for variation between sites: $F_{2,24} = 2.88$, $p = 0.078$.

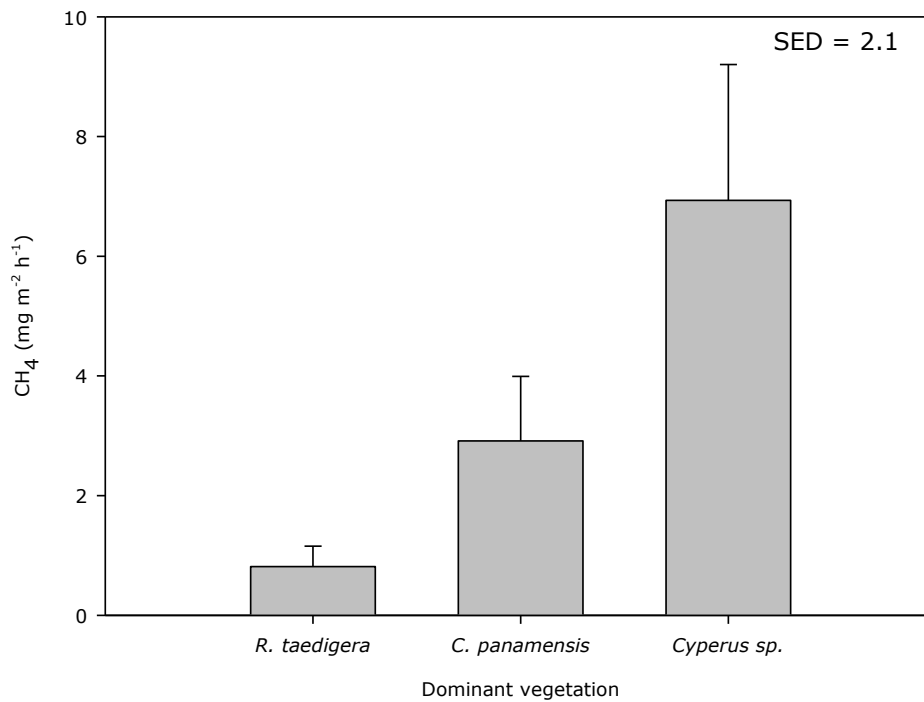


Figure 4.4. Mean CH₄ fluxes from the peat surface at the *R. taedigera*, *C. panamensis* and *Cyperus sp.* sites. Single standard errors of the mean are shown (n=9 replicates). ANOVA test for variation between sites: $F_{2,26} = 4.51$, $p < 0.05$.

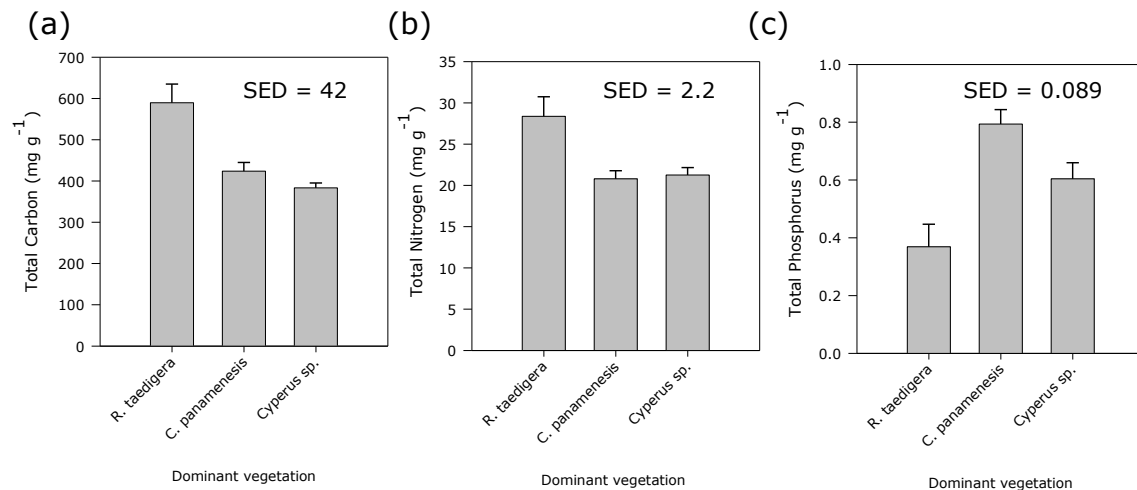


Figure 4.5. Concentrations of total a) carbon, b) nitrogen and c) phosphorus in peat from the *R. taedigera*, *C. panamensis* and *Cyperus sp.* sites. Mean and single standard errors of the mean are shown (n=9). ANOVA test for variation between sites:

- a) $F_{2,26} = 13.45$, $p < 0.001$
- b) $F_{2,26} = 7.33$, $p < 0.05$
- c) $F_{2,26} = 10.47$, $p < 0.001$

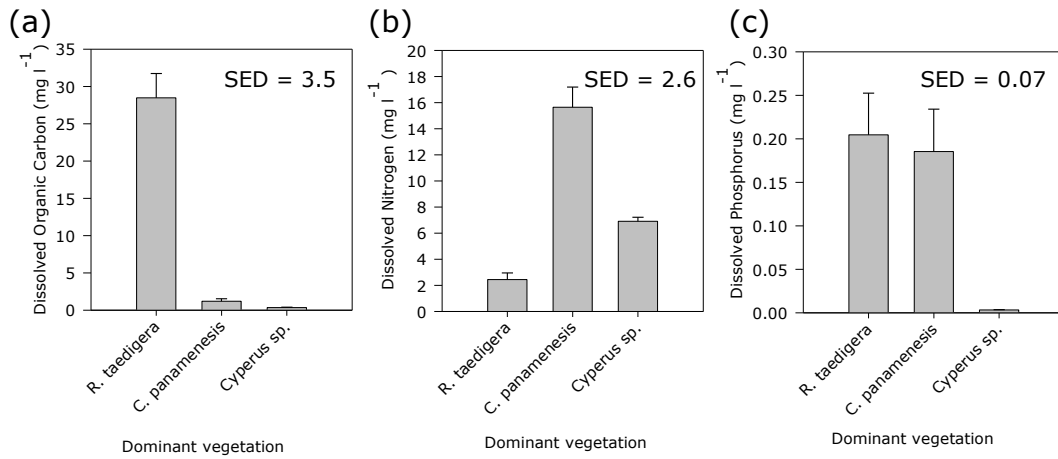


Figure 4.6. Mean concentrations of dissolved a) C (DOC), b) N (DN) and c) P (DP) in the surface water from the *R. taedigera*, *C. panamensis* and *Cyperus sp.* sites. Single standard errors of the mean are shown (n=9). ANOVA test for variation between sites:

a) $F_{2,20} = 50.76$, $p < 0.001$

b) $F_{2,20} = 13.00$, $p < 0.001$

c) $F_{2,19} = 4.29$, $p < 0.05$

4.3.2 Factors controlling in situ CO₂ and CH₄ fluxes

When the data for the three sites were analysed together, a strong positive co-variation between CO₂ and CH₄ fluxes was apparent (Fig. 4.7). although this trend was not apparent ($p > 0.05$) on an individual site basis. Furthermore, there was a trend for greater release of CO₂ from locations where the water table was above the peat surface (Fig. 4.8). The height of the water table accounted for 12% of the variation in CO₂ flux. However, for individual sites there was no correlation between the water table and CO₂ flux ($p > 0.05$). In contrast, CH₄ flux was unaffected by the height of the water table ($F_{1,26} = 64.54$, $p = 0.1$). No overall effects of either total or dissolved C, N and P on CO₂ and CH₄ fluxes were detected.

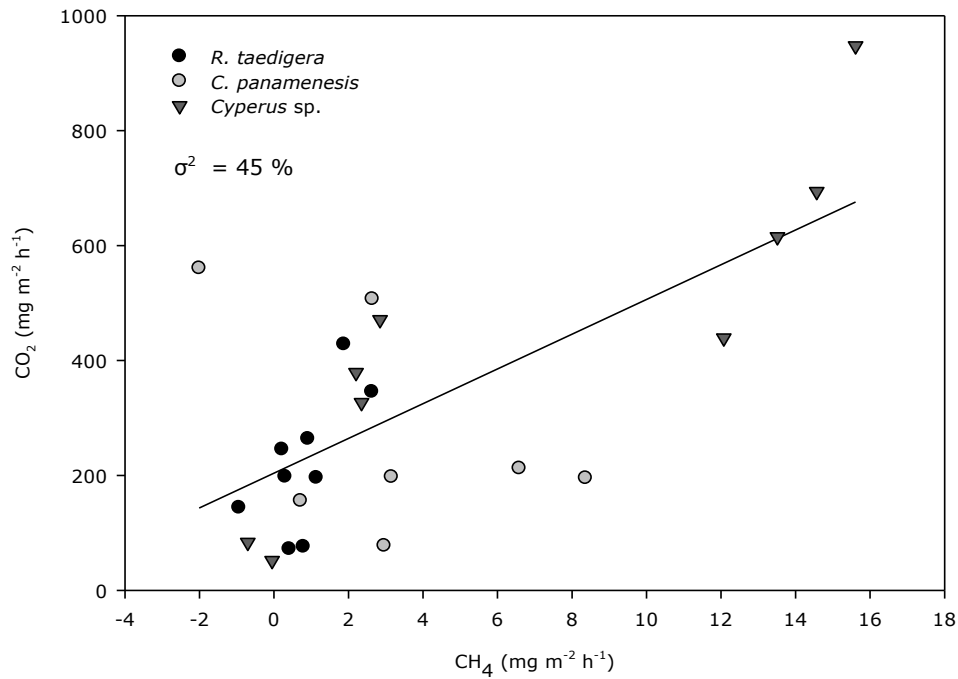


Figure 4.7. Linear regression between CO_2 and CH_4 fluxes for the *R. taedigera*, *C. panamensis* and *Cyperus sp.* sites. Regression analysis: $F_{1,24} = 20.27$, $p < 0.001$.

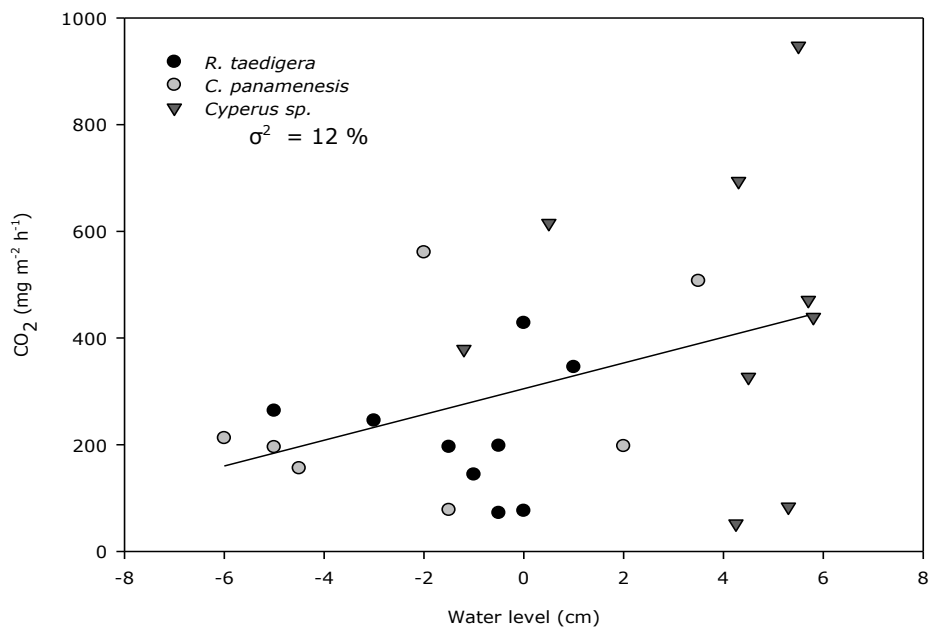


Figure 4.8. Linear correlation between CO_2 flux and the level of the peat surface in relation to the water table for the *R. taedigera*, *C. panamensis* and *Cyperus sp.* sites. Positive values (cm) indicate the distance between the water table and the top of individual hummocks while negative values indicate the depth between the water table and the submerged peat surface in hollows. Regression analysis: $F_{1,24} = 4.20$, $p = 0.052$.

4.3.2.1 Impact of total C, N and P content of peat on spatial variation in gas fluxes

No significant effects of variation in the total C, N and P concentrations of peat or their ratios on CO₂ or CH₄ fluxes were detected within sites (Tables 4.1-4.4).

4.3.2.2 Impact of dissolved C, N and P in surface water on spatial variation in gas fluxes

The positive relationship between CO₂ fluxes and dissolved organic carbon (DOC) in the surface water at the *R. taedigera* site approached significance ($p=0.07$; Fig. 4.9a), whereas CO₂ fluxes showed no correlation with DOC at the *C. panamensis* and *Cyperus* sp. sites (Fig. 4.9b-c).

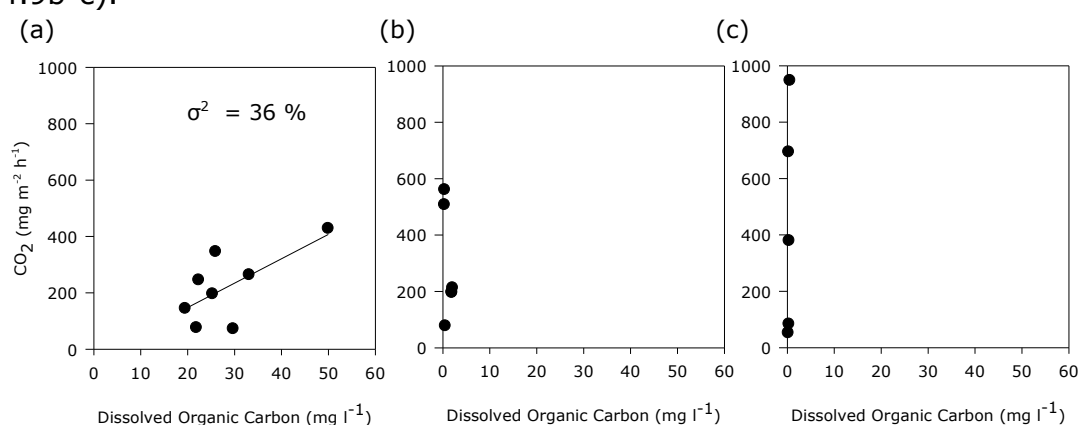


Figure 4.9. Relationship between CO₂ flux and dissolved organic C (DOC) concentration for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,7} = 4.87$, $p = 0.07$
- b) $F_{1,5} = 1.79$, $p = 0.3$
- c) $F_{1,4} = 2.82$, $p = 0.2$

At the *C. panamensis* site, significant positive correlations between CO₂ flux and the DOC:DP and DN:DP ratios in the surface water were detected (Figs. 4.10b, 4.11b). Dissolved C:P ratios at this site (0.05–23.9) were much lower than at either the *R. taedigera* (45.2–507.5) or *Cyperus* sp. sites (85.0–240.4). The positive correlation between CO₂ flux and dissolved N:P ratio at the *C. panamensis* site accounted for 77% of the variance. No further significant relationships between CO₂ fluxes and the nutrient status of the surface water were found for any of the sites examined (Tables 4.5 and 4.6).

Table 4.1. Analysis of total C, N and P concentrations in the surface peat and their effects on CO₂ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics.

Site	C (mg g ⁻¹)			N (mg g ⁻¹)			P (mg g ⁻¹)		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	589 \pm 45	424 \pm 21	383 \pm 12	28.4 \pm 2.4	20.8 \pm 1.0	21.3 \pm 0.9	0.37 \pm 0.08	0.79 \pm 0.05	0.60 \pm 0.06
<i>F</i>	0.02	0.81	0.39	0.48	1.05	0.54	0.10	0.04	1.42
<i>p</i>	0.9	0.4	0.6	0.5	0.4	0.5	0.8	0.9	0.3
σ^2 (%)	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.2. Analysis of total C, N and P concentrations in the surface peat and their effects on CO₂ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics.

Site	C:N			C:P			N:P		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	21 \pm 1	21 \pm 1	18 \pm 1	2040 \pm 295	552 \pm 45	680 \pm 64	98 \pm 14	26 \pm 2	38 \pm 4
<i>F</i>	1.53	4.09	1.85	0.22	0.08	1.74	0.9	0.64	0.58
<i>P</i>	0.3	0.1	0.2	0.7	0.8	0.2	0.4	0.5	0.5
σ^2 (%)	ns	34.0	ns	ns	ns	ns	ns	ns	ns

Table 4.3. Analysis of total C, N and P concentrations in the surface peat and their effects on CH₄ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics.

Site	C (mg g ⁻¹)			N (mg g ⁻¹)			P (mg g ⁻¹)		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	589 \pm 45	424 \pm 21	383 \pm 12	28.4 \pm 2.4	20.8 \pm 1.0	21.3 \pm 0.9	0.37 \pm 0.08	0.79 \pm 0.05	0.60 \pm 0.06
<i>F</i>	0.49	3.59	0.49	0.00	4.00	0.03	0.53	0.39	0.53
<i>P</i>	0.5	0.1	0.5	1.0	0.1	0.9	0.5	0.6	0.5
σ^2 (%)	ns	24.5	ns	ns	27.3	ns	ns	ns	ns

Table 4.4. Analysis of total C, N and P ratios of the surface peat and their effect on CH₄ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9) with *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold.

Site	C:N			C:P			N:P		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	21 \pm 1	21 \pm 1	18 \pm 1	2040 \pm 295	552 \pm 45	680 \pm 64	98 \pm 14	26 \pm 2	38 \pm 4
<i>F</i>	1.68	0.00	0.06	0.08	0.33	0.03	0.78	0.29	0.63
<i>P</i>	0.2	1.0	0.8	0.8	0.6	0.9	0.4	0.6	0.5
σ^2 (%)	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.5. Analysis of the effect of dissolved C (DOC), N (DN) and P (DP) concentrations in the surface water on CO₂ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics and near significant relationships are shown in italics.

Site	DOC (mg l ⁻¹)			DN (mg l ⁻¹)			DP (mg l ⁻¹)		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	28.48 \pm 3.24	1.32 \pm 0.33	0.35 \pm 0.04	2.4 \pm 0.5	15.6 \pm 1.5	6.9 \pm 0.3	0.205 \pm 0.048	0.209 \pm 0.047	0.003 \pm 0.0011
<i>F</i>	4.87	1.79	2.82	3.42	0.51	3.60	0.07	1.76	0.04
<i>P</i>	<i>0.070</i>	0.3	0.2	0.1	0.5	0.2	0.8	0.3	0.9
σ^2 (%)	35.6	ns	ns	25.7	ns	ns	ns	ns	ns

Table 4.6. Analysis of the effect of dissolved C (DOC), N (DN) and P (DP) ratios of the surface water on CO₂ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics; near significant relationships are shown in italics.

Site	DOC:DN			DOC:DP			DN:DP		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	13.58 \pm 1.63	0.09 \pm 0.01	0.05 \pm 0.01	220 \pm 58	9 \pm 2	119 \pm 23	18 \pm 6	181 \pm 91	2326 \pm 217
<i>F</i>	0.48	1.67	3.76	1.14	17.95	2.61	2.27	18.86	0.28
<i>P</i>	0.5	0.3	0.2	0.3	< 0.05	0.2	0.2	< 0.05	0.6
σ^2 (%)	ns	ns	ns	ns	77.2	ns	ns	78.1	ns

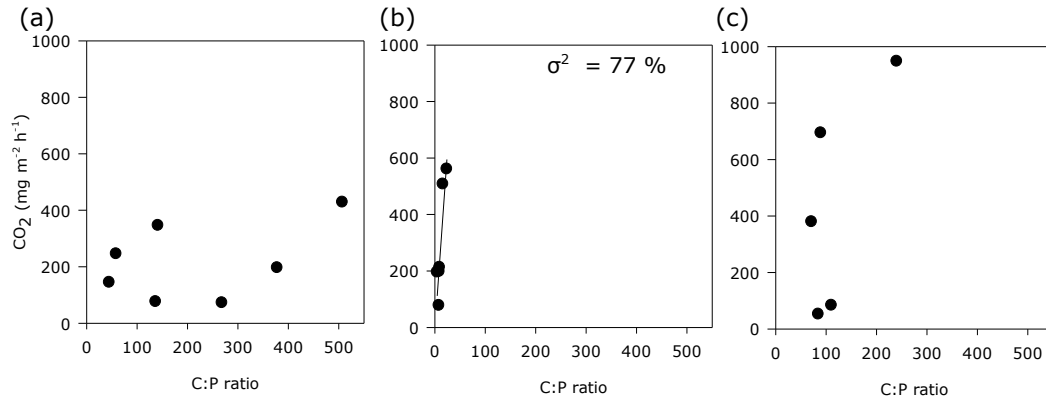


Figure 4.10. Relationship between CO₂ flux and dissolved C:P ratio for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,6} = 1.14$, $p=0.3$
- b) $F_{1,5} = 17.95$, $p<0.05$
- c) $F_{1,4} = 2.61$, $p=0.2$

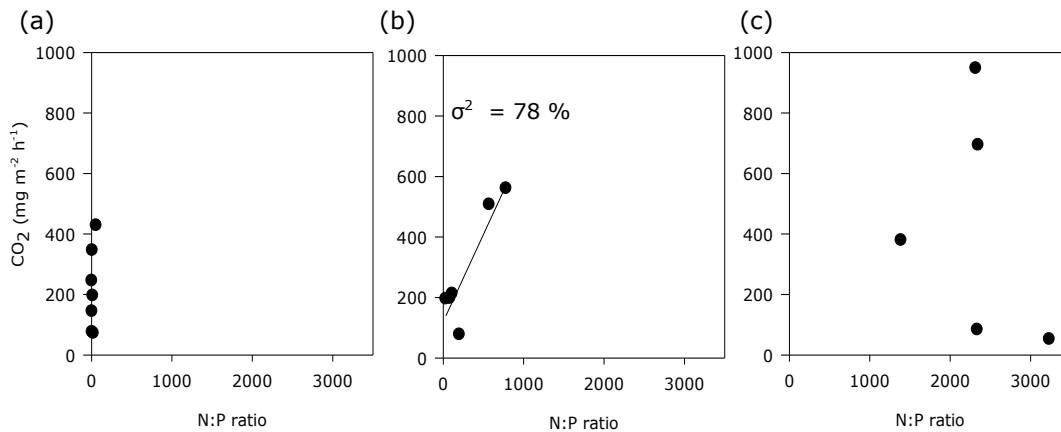


Figure 4.11. Relationship between CO₂ flux and N:P ratio for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,6} = 2.27$, $p=0.2$
- b) $F_{1,5} = 18.86$, $p<0.05$
- c) $F_{1,4} = 0.28$, $p=0.6$

CH₄ fluxes were significantly correlated with surface water chemistry only at the *C. panamensis* site, where DOC, DN and DP concentration accounted for a substantial fraction of the variation in CH₄ flux (47, 68 and 37 % of the variance respectively; Figs. 4.12b, 4.13b, 4.14b). Surface water chemistry (i.e. C, N and P concentrations and their ratios) had no significant effects on CH₄ flux at the *R. taedigera* and *Cyperus* sp. sites (Tables 4.7, 4.8). No other significant correlations between CH₄ flux and surface water characteristics were detected.

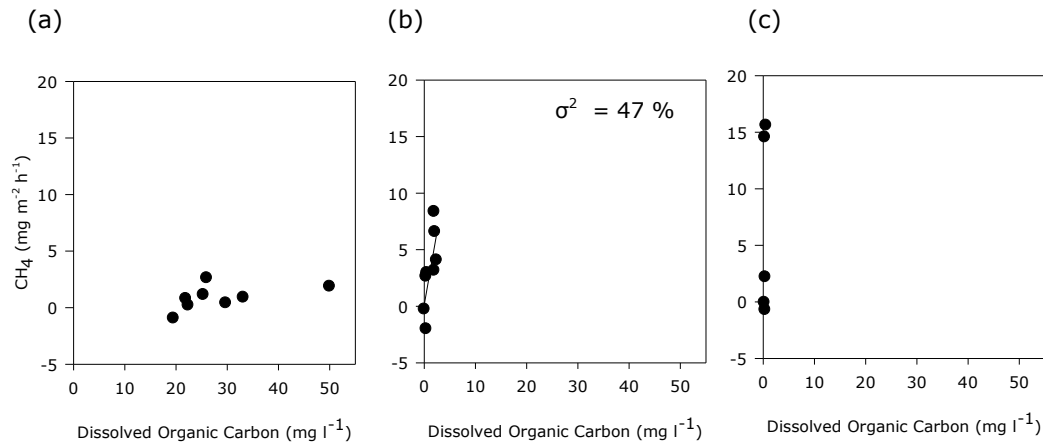


Figure 4.12. Relationship between CH₄ flux and dissolved C (DOC) concentration for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,7} = 2.03$, $p=0.2$
- b) $F_{1,7} = 7.32$, $p<0.05$
- c) $F_{1,4} = 1.01$, $p=0.4$

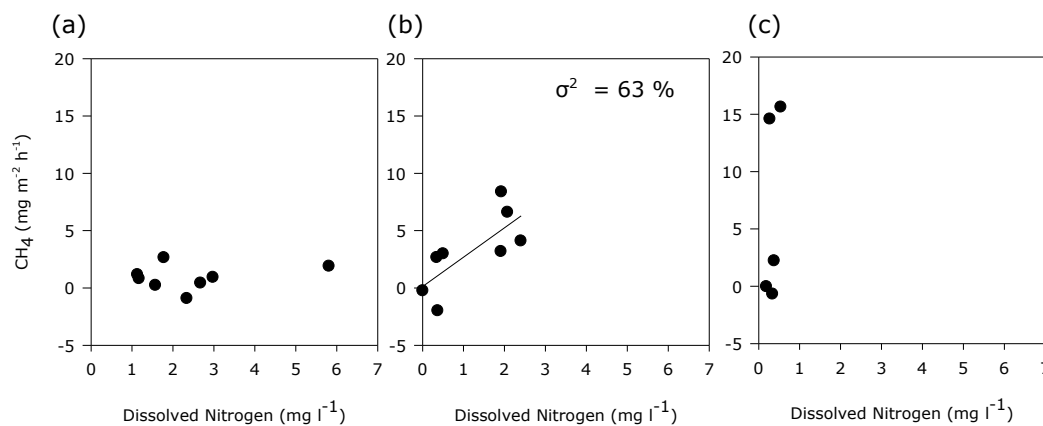


Figure 4.13. Relationship between CH₄ flux and dissolved N (DN) concentration for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,6} = 0.34$, $p=0.6$
- b) $F_{1,7} = 12.87$, $p<0.05$
- c) $F_{1,4} = 2.27$, $p=0.2$

4.3.3 Spatial variation in CO₂ and CH₄ fluxes at the *R. taedigera* site

There was no significant variation in CO₂ fluxes between the two locations examined at the *R. taedigera* site (Fig. 4.15), although the range of fluxes was greater at site A (0.5–1021.5 mg m⁻² h⁻¹) than at site B (63.6–819.2 mg m⁻² h⁻¹); however, the means were similar at both sites, indicating

that although site A had a greater range the typical flux from each site was similar.

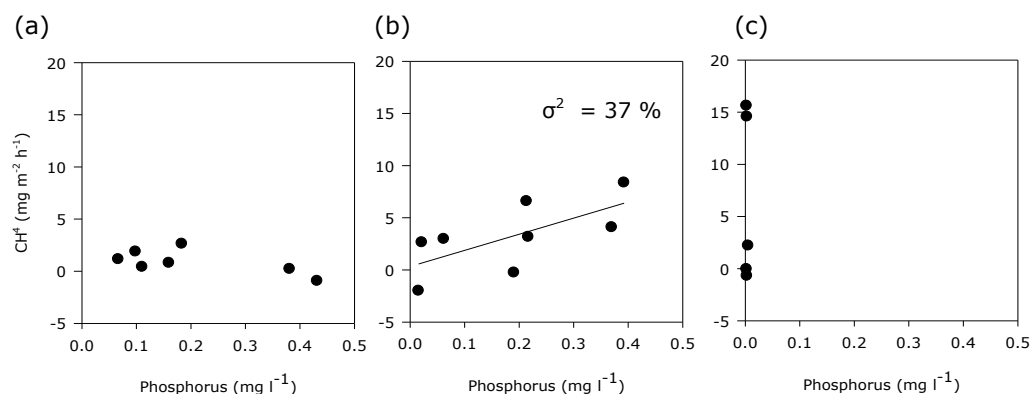


Figure 4.14. Relationship between CH₄ flux and dissolved P (DP) concentration for the a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. sites. Regression analysis:

- a) $F_{1,6} = 3.84$, $p=0.1$
- b) $F_{1,7} = 5.03$, $p=0.066$
- c) $F_{1,4} = 0.27$, $p=0.6$

There was no overall effect of tree or ring (tree: $F_{2,61} = 0.86$, $p=0.4$; ring: $F_{2,61} = 1.49$, $p=0.2$). However there was a near significant interaction of tree and ring ($F_{2,61} = 3.10$, $p=0.055$), due to a significant interaction at site A (Fig. 4.16a) and a significant ring effect at site B (Fig. 4.16b). Fluxes were then analysed using the factors C, N and P (both total, dissolved and ratios) as covariates. There were significant effects of site and ring on CO₂ fluxes when the following factors were used as covariates: DP ($F_{2,43} = 1.00$), DN ($F_{2,43} = 1.00$), DN:DP ($F_{2,43} = 0.91$), DOC:DP ($F_{2,43} = 0.92$) and DOC:DN ($F_{2,43} = 0.95$) all had p values <0.05 . There was a near significant effect of DOC ($F_{2,43} = 0.98$, $p=0.058$). For all factors, Site A showed a tendency for range of CO₂ fluxes to increase with increasing distance from the tree (increasing ring number; Ring 1: 54.7 - 410.9 mg m⁻² h⁻¹; Ring 2: 9.5 - 724.4 mg m⁻² h⁻¹; Ring 3: 63.6 - 1021.5 mg m⁻² h⁻¹), whereas site B exhibited the opposite tendency as the range of fluxes decreased with increasing distance (Ring 1: 11.7 - 819.2; Ring 2: 63.6 - 352.4 mg m⁻² h⁻¹; Ring 3: 108.8 - 404.9 mg m⁻² h⁻¹).

Table 4.7. Analysis of the effect of dissolved C (DOC), N (DN) and P (DP) concentrations in the surface water on CH₄ fluxes for the 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. sites. Mean concentrations \pm SEM (n=9 replicates), *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics; near significant relationships are shown in italics.

Site	DOC (mg l ⁻¹)			DN (mg l ⁻¹)			DP (mg l ⁻¹)		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	28.48 \pm 3.24	1.32 \pm 0.33	0.35 \pm 0.04	2.4 \pm 0.5	15.6 \pm 1.5	6.9 \pm 0.3	0.205 \pm 0.048	0.209 \pm 0.047	0.003 \pm 0.0011
<i>F</i>	2.03	15.80	1.01	0.34	12.78	2.27	3.84	5.03	0.27
<i>P</i>	0.2	< 0.05	0.4	0.6	< 0.05	0.2	0.1	<i>0.066</i>	0.6
σ^2 (%)	ns	47.4	ns	ns	62.7	ns	ns	36.6	ns

Table 4.8. Analysis of C, N and P ratios of the surface water and the affect on CH₄ fluxes at sites; 1) *R. taedigera*, 2) *C. panamensis* and 3) *Cyperus* sp. Average concentrations \pm SE (n = 9 replicates) with *F* and *p* values where applicable and σ^2 when significant. Significant relationships are shown in bold and italics. Near significant relationships are shown in italics.

Site	DOC:DN			DOC:DP			DN:DP		
	1	2	3	1	2	3	1	2	3
Mean \pm SEM	13.58 \pm 1.63	0.09 \pm 0.01	0.05 \pm 0.01	220 \pm 58	9 \pm 2	119 \pm 23	18 \pm 6	181 \pm 91	2326 \pm 217
<i>F</i>	0.37	5.54	1.59	1.65	0.50	1.75	1.05	2.57	0.02
<i>P</i>	0.6	<i>0.057</i>	0.3	0.3	0.5	0.3	0.4	0.2	0.9
σ^2 (%)	ns	39.4	ns	ns	ns	ns	ns	ns	ns

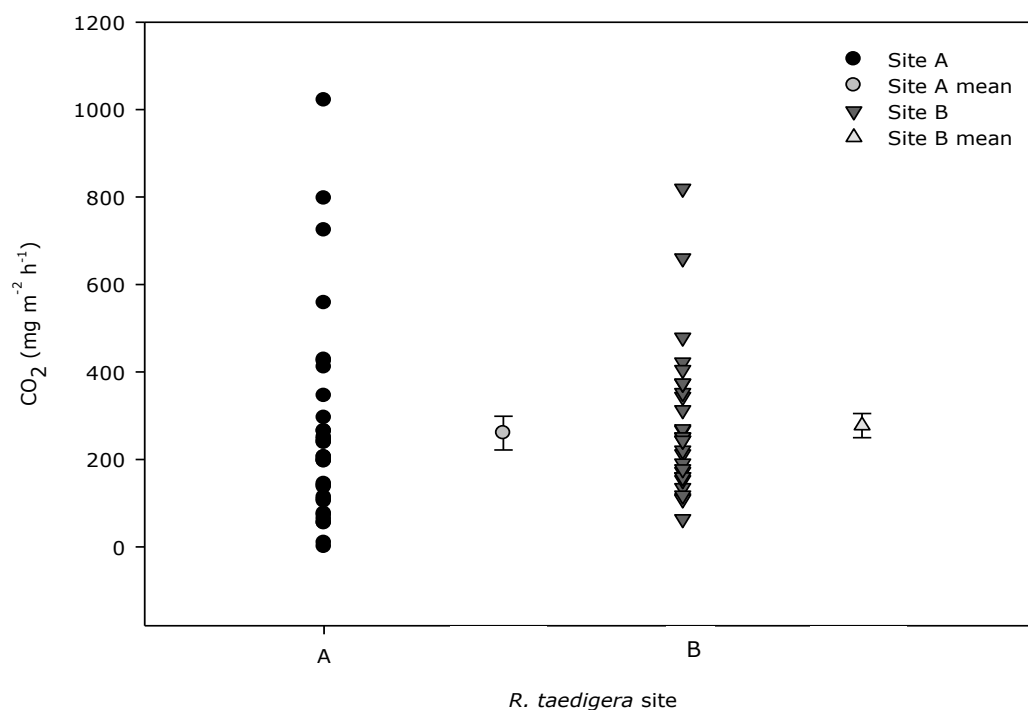


Figure 4.15. CO₂ fluxes at location A and B at the *R. taedigera* site, the figure show the range of the individual measurements at each site and mean values with double standard errors of the mean. ANOVA of Site differences: $F_{1,61} = 0.07$, $p=0.8$.

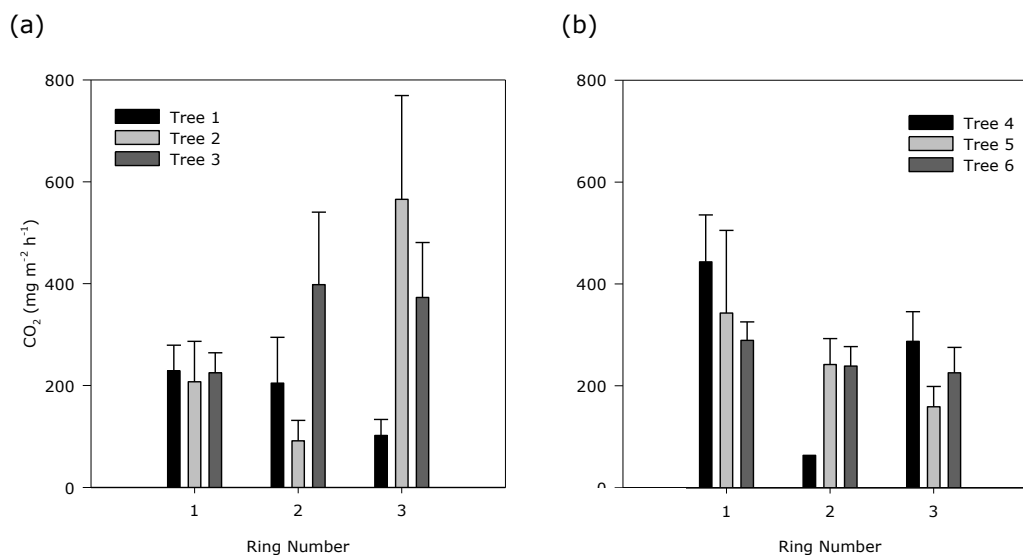


Figure 4.16. Influence of distance from *R. taedigera* trees on CO₂ fluxes at Sites A (a) and B (b). Single standard errors of the mean are shown ($n=??$). ANOVA analysis of variance:

- a) Tree: $F_{2,32} = 1.80$, $p=0.2$
 Ring: $F_{2,32} = 1.41$, $p=0.3$
 TreexRing: $F_{4,32} = 2.87$, $p<0.05$
 b) Tree: $F_{2,28} = 0.04$, $p=0.9$
 Ring: $F_{2,28} = 3.76$, $p<0.05$
 TreexRing: $F_{4,28} = 1.49$, $p=0.2$

No significant effects of Site, Ring number, Tree or interactions between these factors on CH₄ fluxes were detected. The range of fluxes was generally greater at site A (-1.5 to 6.0 mg m⁻² h⁻¹) than at site B (-1.4 to 2.1 mg m⁻² h⁻¹) with the exception of one outlying value of 6.0 mg m⁻² h⁻¹ (Fig. 4.17). The addition of C, N and P as covariates in the statistical analysis provided no significant improvement of fit.

4.3.4 Effects of temperature and nutrient treatments on CO₂ efflux from ex situ peat samples at field capacity

4.3.4.1 Impacts of temperature on CO₂ efflux

The ex situ CO₂ efflux was greatest for peat from the *Cyperus* sp. site, followed successively by the *R. taedigera* and *C. panamensis* sites at all three incubation temperatures (site effect: F_{2, 58} = 15.42, P < 0.001); Fig. 4.17). As expected, CO₂ production increased with temperature for all three peat types (F_{2,58} = 3.82, p<0.05) (Fig. 4.18). There was no significant interaction between Site and Temperature (F_{4,58} = 1.38, p>0.05). However, the magnitude of the temperature response varied substantially between sites. The strongest effect was found at the *R. taedigera* site (Fig. 4.18a) with a c. 300 % increase in CO₂ production over the 10 °C incubation range, while at the *C. panamensis* site (Fig. 4.18b) the impact of the increased temperature was marginal.

4.3.4.2 Effects of nutrient treatment on CO₂ flux over a range of temperatures

The influence of nutrient amendment differed between incubation temperatures. There were no significant effects of nutrient treatment or site*nutrient treatment interaction at 22 °C (Amendments: F_{6,111} = 0.43, p>0.05; Interactions: F_{12,111} = 1.04, p>0.05), whereas at 27 °C, close to the normal *in situ* surface peat temperature, there was a significant site x nutrient treatment interaction (F_{12,130} = 2.79, p<0.05) but no overall significant effect of nutrient amendment. At 32 °C there was a significant effect of site (F_{2,129} = 21.86, p<0.001) and nutrient amendment (F_{6,129} =

2.37, $p < 0.05$), but no significant interaction effect ($F_{12,129} = 1.09$, $p > 0.05$).

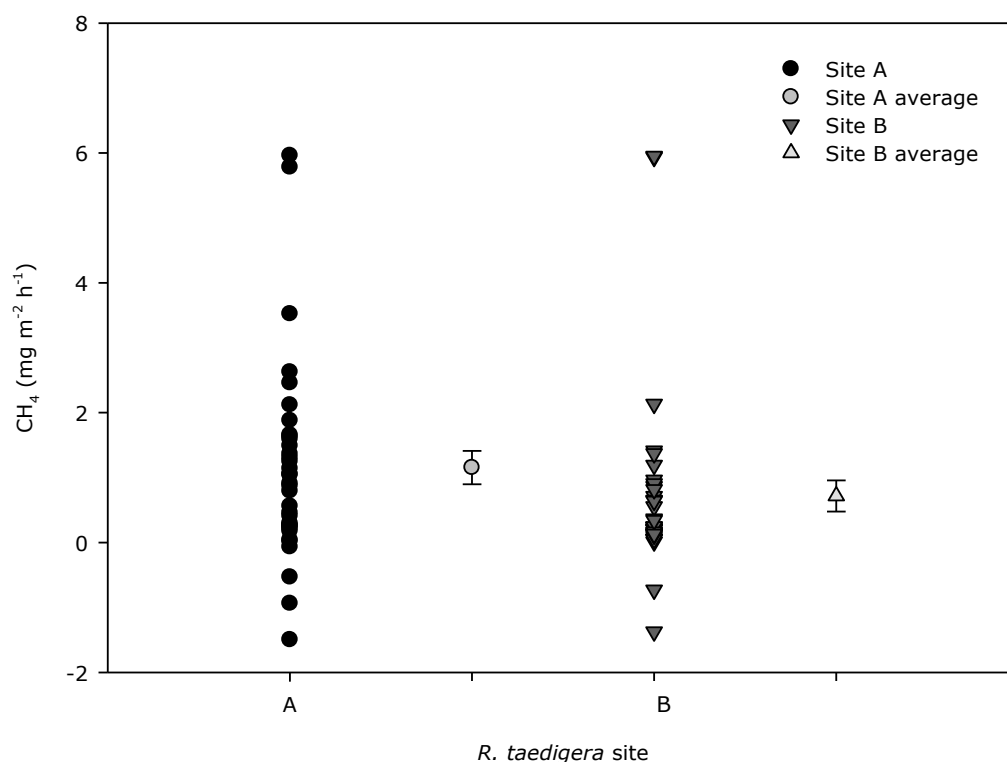


Figure 4.17. CH₄ fluxes at locations A and B at the *R. taedigera* site showing the range of individual measurements at each site and mean values with double standard errors of the mean. ANOVA of Site differences: $F_{1,69} = 1.54$, $p = 0.2$.

The influence of nutrient amendment differed between incubation temperatures. Thus, there were no significant effects of nutrient treatment or site*nutrient treatment interactions at 22 °C (Amendments: $F_{6,111} = 0.43$, $p > 0.05$; Interactions: $F_{12,111} = 1.04$, $p > 0.05$), whereas at 27 °C, close to the normal *in situ* surface peat temperature, there was a significant site*nutrient treatment interaction ($F_{12,130} = 2.79$, $p < 0.05$) but no overall significant effect of nutrient amendment.

Table 4.9. ANOVA to establish the effect of total C, N and P concentrations and their ratios, dissolved C (DOC), N (DN) and P (DP) and their ratios on CO₂ flux overall and individually at Site A and B within the *R. taedigera* site. *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics; near significant relationships are shown in italics

		Peat			Peat Ratios			Surface Water			Surface water ratios		
		Total C	Total N	Total P	C:N	C:P	N:P	DOC	DN	DP	DOC:DN	DOC:DP	DN:D P
Overall	<i>F</i>	0.41	0.25	0.94	0.21	0.00	1.86	0.08	0.08	0.62	0.22	0.47	0.46
	<i>P</i>	0.5	0.6	0.3	0.6	1.0	0.2	0.8	0.8	0.4	0.6	0.5	0.5
	σ^2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	(%)												
Site A	<i>F</i>	0.02	0.00	0.58	0.49	0.16	0.32	0.05	0.06	0.06	0.01	0.12	0.59
	<i>P</i>	0.9	1.0	0.5	0.5	0.7	0.6	0.8	0.8	0.8	0.9	0.7	0.4
	σ^2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	(%)												
Site B	<i>F</i>	7.89	2.79	0.00	2.80	0.92	0.96	0.78	1.60	2.30	1.66	0.92	0.96
	<i>P</i>	<0.05	0.1	1.0	0.1	0.4	0.3	0.4	0.2	0.1	0.2	0.4	0.3
	σ^2	23.9	7.5	ns	7.6	ns	ns	ns	ns	6.7	ns	ns	ns
	(%)												

Table 4.10. ANOVA to establish the effect of the total C, N and P concentrations and their ratios, dissolved C (DOC), N (DN) and P (DP) and their ratios, on CH₄ flux both overall and individually at Site A and B within the *R. taedigera* site. *F* and *P* values and σ^2 are shown where applicable. Significant relationships are shown in bold italics; near significant relationships are shown in italics.

	Site	Peat			Peat Ratios			Surface Water			Surface water ratios		
		C (mg g ⁻¹)	N (mg g ⁻¹)	P (mg g ⁻¹)	C:N	C:P	N:P	C (mg l ⁻¹)	N (mg l ⁻¹)	P (mg l ⁻¹)	C:N	C:P	N:P
Overall	<i>F</i>	0.30	0.45	0.80	0.07	0.79	0.99	0.55	0.06	0.72	0.10	0.28	0.31
	<i>P</i>	0.6	0.5	0.4	0.8	0.4	0.3	0.5	0.8	0.4	0.8	0.6	0.6
	σ^2 (%)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Site A	<i>F</i>	0.00	0.05	0.22	0.71	0.85	0.53	0.11	1.27	3.18	1.48	0.21	0.09
	<i>P</i>	1.0	0.8	0.6	0.4	0.4	0.5	0.8	0.3	<i>0.087</i>	0.2	0.7	0.8
	σ^2 (%)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	8.0	n/a	n/a	n/a
Site B	<i>F</i>	0.09	0.14	0.91	0.00	0.52	0.27	1.24	0.76	0.24	0.11	0.15	0.17
	<i>P</i>	0.8	0.7	0.4	1.0	0.5	0.6	0.3	0.4	0.6	0.7	0.7	0.7
	σ^2 (%)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

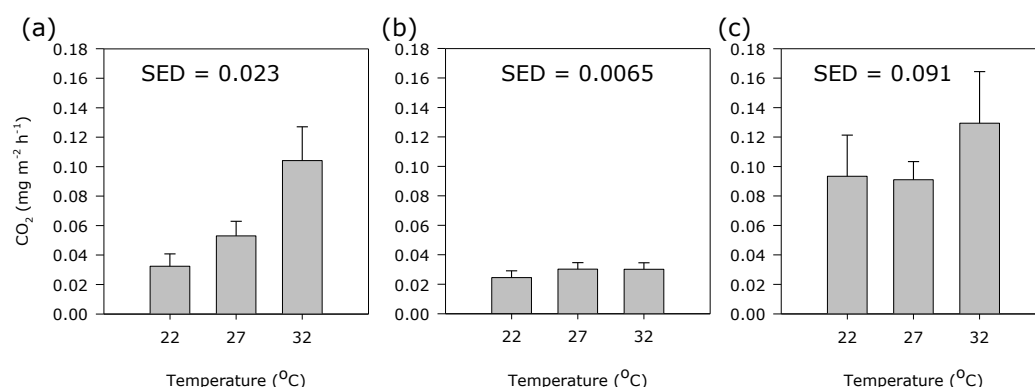


Figure 4.18 CO₂ fluxes from control peat samples at 22, 27 and 32 °C for a) *R. taedigera* b) *C. panamensis* and c) *Cyperus* sp. Means + single standard errors of the mean (n=8 for *R. taedigera* and *C. panamensis* and n=6 replicates for *Cyperus* sp.). Unbalanced ANOVA analysis:

a) $F_{2,19} = 5.07$, $p < 0.05$

b) $F_{2,22} = 0.52$, $p = 0.6$

c) $F_{2,15} = 0.54$, $p = 0.6$

The interaction effect of site*nutrient amendment is driven by the lack of effect of the nutrient amendments on CO₂ efflux from peat from the *R. taedigera* and *Cyperus* sp. sites, whereas nutrient amendment of peat from the *C. panamensis* site significantly affected CO₂ flux (Fig. 4.19). Interestingly, none of the nutrient treatments increased CO₂ fluxes above control samples. CO₂ fluxes in both P treatments and the combined high N and P amendments were greater than under solely N amendment (both high and low). At 32 °C, there was a significant effect of nutrient amendment on CO₂ flux ($F_{6,129} = 2.40$, $p < 0.05$) across all three peat types similar to that found at the *C. panamensis* site at 27 °C, and no site x nutrient treatment interaction was observed at the highest temperature ($F_{12,129} = 1.43$, $p > 0.05$).

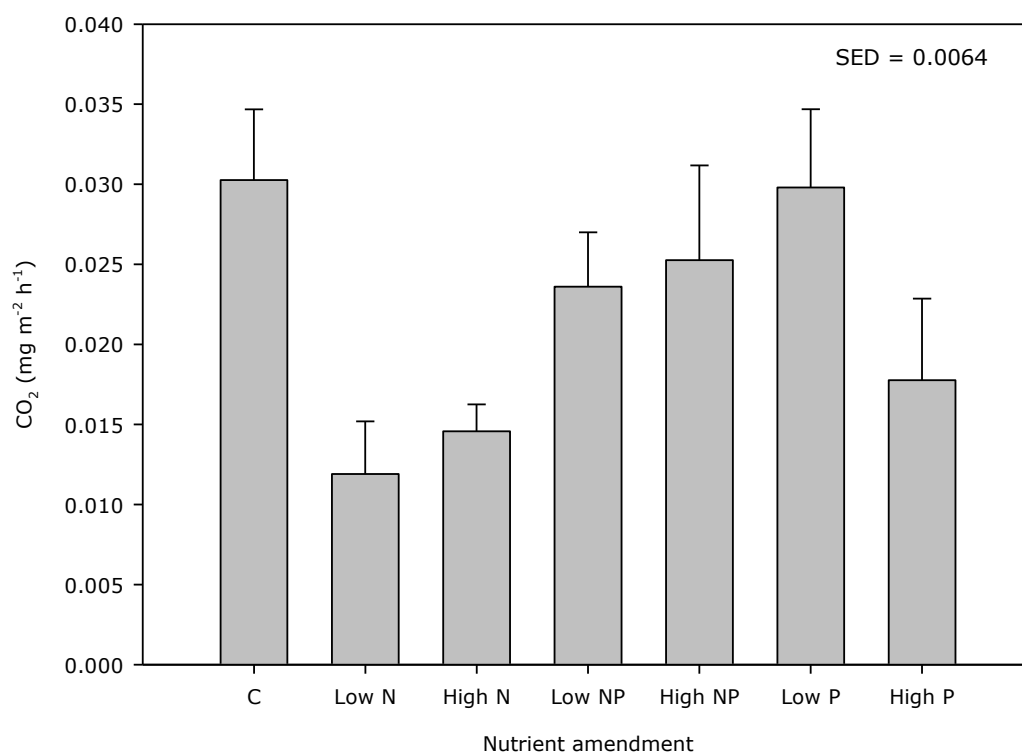


Figure 4.19. CO₂ fluxes from peat from the *C. panamensis* site following different nutrient amendments and incubation at 27 °C. Nutrient amendments included a control, low and high levels of nitrogen (N), phosphorus (P) and combined N and P applications. Means and single standard errors of the mean are shown. Unbalanced ANOVA: $F_{6,47} = 2.78$, $p < 0.05$.

4.4 Discussion

4.4.1 Across site variation

CO₂ and CH₄ fluxes for peat from the *Cyperus* sp. site were greater than from either of the other sites (Figs. 4.3 and 4.4), and the *ex situ* CO₂ flux was also greatest for peat from this site (Fig. 4.18). Wright *et al.* (2011) have shown that *ex situ* CO₂ and CH₄ fluxes were greatest throughout the peat profile at the *Cyperus* sp. site and showed a strong link between the production of both gases and the quantity of carbohydrates present in the peat. Indeed, carbohydrate concentration in surface peat at the *Cyperus* sp. site was c. 50 % greater than at the *R. taedigera* site. However, the high *in situ* gas production at this site is somewhat unexpected due to the low DOC, DP and total C and N concentrations within the peat; high CO₂ and CH₄ fluxes are more typically associated with naturally high C, N and P concentrations (Wright and Reddy, 2001; Yavitt *et al.*, 2005), although a study by Aerts and Toet (1997) suggested that, in some cases, the addition of excess nutrients may suppress gas production within peat. It is possible that the timing of measurements (c. 1000 h, 1130 h and 1230 h for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites respectively) for the *in situ* sampling measurements may be partly responsible for the greater CO₂ and CH₄ fluxes at the *Cyperus* sp. site, as greater fluxes have been found later during the diurnal period at this site compared to the other two sites. *C. panamensis* followed a similar diurnal pattern to that seen at the *Cyperus* sp. site but, as this site was sampled earlier in the day than the *Cyperus* sp. site, it is likely that fluxes from the *C. panamensis* site were less than the potential daily maximum, whilst those for the *Cyperus* sp. site provide a more accurate representation of the daily maximum flux (*cf.* Section 5.3.2).

Interestingly, there was a trend over all three sites for CO₂ emissions to be greater at locations with standing water on the peat surface (Fig. 4.8). This is reflected by the relationship between high rainfall and CO₂ emissions reported in Section 5.3.2. However, this observation contrasts with much of the literature on wetlands, which suggests that CO₂ emissions are generally higher when the water table is below the peat surface (Furukawa *et al.*, 2005; Hadi *et al.*, 2005; Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b; Hirano *et al.*, 2009;

Couwenberg *et al.*, 2010), thereby promoting aerobic decomposition. The litter decomposition experiments reported in Chapter 7 also show that mass loss was greater under low water table conditions. However, in this context, it is important to bear in mind that, although the level of submersion of the peat varied between sampling locations, this was driven entirely by the microtopography of the site. As the water table was on average at the surface at the time of sampling, the conditions are not fully comparable to studies linking water table depth to CO₂ emission as this generally refers to substantial water table draw down below the surface (e.g. 30-50 cm) (Furukawa *et al.*, 2005; Hadi *et al.*, 2005; Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b; Hirano *et al.*, 2009; Couwenberg *et al.*, 2010). It is also plausible that hollows accumulate litter and that greater amounts of labile dissolved carbon are present in submerged hollows.

The concept of resource availability as opposed to waterlogging as the main driver of the spatial variability of gas fluxes, is further supported by the co-variation in CH₄ and CO₂ fluxes (Fig. 4.7); if these fluxes were driven by the degree of aeration of the peat, there should be a negative relationship between these fluxes as CH₄ replaces CO₂ production under anaerobic conditions. Potentially, the co-variation between the two gases is linked to root activity and biomass, with high release of CO₂ being correlated to high root biomass and activity and hence high levels of root exudation, providing labile substrate to support CH₄ production (Joabsson *et al.*, 1999; Strom *et al.*, 2003; Klumpp *et al.*, 2007).

4.4.2 Within site variation

Within site variation in CO₂ and CH₄ emissions was mainly associated with differences in dissolved C and P in the surface water. The main controls differed between sites, with DOC (as the most labile C substrate) limiting CO₂ production at the *R. taedigera* site, while C:P and the N:P ratios were important drivers of CO₂ production at the *C. panamensis* site (Figs. 4.10, 4.11). It is interesting that CO₂ production increased with increasing nutrient ratios as this suggests that decomposer activity which results in CO₂ production is actually promoted by low P levels (*cf.* Section 7.4). At the *Cyperus* sp. site, none of the measured

covariates accounted for the variation in the gas fluxes, although the positive correlation between CO₂ and CH₄ release strongly suggests that common drivers controlled their production.

With respect to CH₄ fluxes, clear relationships between soil C and nutrient status and CH₄ production were found only at the *C. panamensis* site, where fluxes were correlated with DOC, DN and DP concentrations. The observation that the greatest proportion of variance was associated with dissolved C and N highlights the importance of substrate availability for small scale variation in CH₄ production. In contrast, nutrient availability and DOC concentration appeared to have no impact on the small scale variation in CH₄ production at the *R. taedigera* or *Cyperus* sp. sites, suggesting that the role of these factors varied strongly in response to specific site characteristics such as peat nutrient status and root C inputs.

There is an interesting contrast between the strong relationships between nutrient availability and *in situ* CO₂ and CH₄ fluxes at the *C. panamensis* site and the lack of positive responses of CO₂ production to *ex situ* nutrient addition under drained conditions. This highlights that decomposition pathways differ in their sensitivity to nutrient limitation as the moisture status of the peat changes from waterlogged to drained (Smolders *et al.*, 2002; Kechavarzi *et al.*, 2010).

As mentioned above, the small scale spatial variation in the nutrient status of peat at the *R. taedigera* and *Cyperus* sp. sites did not explain the variation in CO₂ and CH₄ fluxes. It is plausible that roots have an important role in determining within-site variation in gas production (Joabsson *et al.*, 1999; Metcalfe *et al.*, 2007; Fritz *et al.*, 2011). Indeed, the influence of individual trees and proximity to the trunk on CO₂ fluxes (Fig. 4.16) demonstrates that the trees are important drivers of spatial variability in CO₂ evolution from the peat. Furthermore, the decline in CO₂ fluxes with increasing distance from the centre of the palm clumps suggests either that CO₂ release from roots declines towards the edge of the canopy, as the extent of the rooting system is reached and the rooting density decreases (Andrews *et al.*, 1999) and/or as a result of reduced leaf litter inputs at the edge of the canopy (Nunes *et al.*, 2001; Hojjati, *et al.*, 2009;).

The low DP at the *Cyperus* sp. site (Fig. 4.6) indicates depletion of the available P reserves. Indeed, the microbial biomass at this site formed the largest component of the total P pool in surface peat (Sjögersten *et al.*, 2010). As available P is scarce at this site, in combination with relatively lower C abundance and available N, the microbial community will source C, N and P from less labile sources *via* decomposition of plant material (Wright *et al.*, 2009). The increased decomposition of organic material to release C, N and P increases CO₂ and CH₄ emissions as by-products of decomposition and may be an additional factor in explaining the high *ex situ* potential CO₂ fluxes at this site in addition to the high carbohydrate content of the leaf litter/peat (Wright *et al.*, 2011). Indeed, litter of *Cyperus* sp. is known to have a relatively low available P content (*cf.* Chapter 7) compared to the other litter types, but has the highest concentrations of P in the most recalcitrant form, as is discussed in Chapter 7.

The strong effect of temperature on CO₂ emissions is important in view of the 3.5 °C climate warming predicted for the area (Meehl *et al.*, 2007). Increases in mean temperature are often seen as a less important driver of ecological impacts than changes in the water table in tropical wetlands (Hashimoto *et al.*, 2004; Sjögersten *et al.*, 2010), but here we demonstrate that temperature is a strong limiting factor for decomposition under drained conditions. However, sensitivity to temperature appeared to differ strongly between vegetation communities, possibly in response to the availability of nutrients or labile substrates. In fact, the high temperature response of peat from the *R. taedigera* site may be driven by its high nutrient availability (Figs. 4.5, 4.6) and/or the greater amount of highly recalcitrant peat material with a high temperature sensitivity found at this site (Townsend and Vitousek, 1995; Wright *et al.*, 2011).

Overall, CO₂ and CH₄ fluxes varied in relation to the dominant vegetation and hence the C and nutrient status of the peat and surface water associated with each site. On a smaller scale, there was less variation within areas with the same dominant vegetation. However, sites with different dominant vegetation types differed with respect to nutrient controls of *in situ* gas fluxes, suggesting

that the impact of labile C, N and P concentrations on gas fluxes varied between sites of differing dominant vegetation species.

Chapter 5. Temporal variation in CO₂ and CH₄ fluxes on an annual and diurnal basis

5.1 Introduction

The production of carbon dioxide (CO₂) and methane (CH₄) in peatlands depends on various factors including substrate availability, water table depth (hydrology), soil and air temperature and the type of vegetation present. Temporal variation in CO₂ and CH₄ effluxes on different time scales influence net emissions from specific ecosystems. In northern peatlands, there is evidence of strong interannual, seasonal and diurnal trends in emissions linked to variation in temperature and the activity of the vegetation (Oechel *et al.*, 1993; Whiting and Chanton, 1993; Thomas *et al.*, 1996; Clair *et al.*, 2002; Turetsky *et al.*, 2002; Ding *et al.*, 2005; Coursolle *et al.*, 2006). In tropical peatlands, annual fluctuations in soil and air temperatures are smaller than in boreal and northern peatlands (Jauhien *et al.*, 2005; Hirano *et al.*, 2009), with the result that temperature is less important in determining temporal variation in CO₂ and CH₄ fluxes, although higher temperatures increase decomposition rates (Kadlec and Reddy, 2001; Couwenburg *et al.*, 2010). In tropical systems, hydrology (Hadi *et al.*, 2005; Hashimoto *et al.*, 2007; Jauhien *et al.*, 2008; Strack *et al.*, 2008; Couwenburg *et al.*, 2010), substrate availability and associated links with dominant vegetation type (Updegraff *et al.*, 1995; Scanlon *et al.*, 2000; Wright and Reddy, 2007; Wright *et al.*, 2011) are the foremost factors influencing CO₂ and CH₄ fluxes from the peat surface to the atmosphere.

With respect to temporal variability *per se*, strong seasonal trends in CO₂ and CH₄ fluxes may occur in response to seasonal variation in rainfall. During the dry season, the water table may fall substantially below the peat surface and this generally tends to increase CO₂ emissions and

reduce CH₄ fluxes (Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b). Seasonal variation in temperature may also influence CO₂ emissions from tropical peatlands and, although this often amounts to a few degrees centigrade, it contributes further to the seasonal trends in gas emissions in SE Asia (Hirano *et al.*, 2009).

In addition to abiotic controls on heterotrophic respiration, vegetation has an important role in controlling CO₂ and CH₄ production and release and influences temporal variation in gas production through several processes. Input of fresh organic material from dead roots (Hanson *et al.*, 2000; Personeni and Loiseau, 2004; Crow and Wieder, 2005) and release of photoassimilates as root exudates into the peat profile supply the microbial community with labile substrate, increasing the production of both CO₂ and CH₄ (Joabsson *et al.*, 1999; Schwendenmann *et al.*, 2006; Klumpp *et al.*, 2007; Konnerup *et al.*, 2010). Furthermore, root respiration *per se* is a direct source of CO₂ which contributes up to 50 % of the CO₂ released from tropical forests (Crow and Wieder, 2005; Schwendenmann and Veldkamp, 2006; Metcalfe *et al.*, 2008). Roots may also influence the redox potential of the soil and hence CH₄ emissions through the release of O₂ (Fritz *et al.*, 2011).

Below-ground impacts of plants on gas fluxes are, in part, linked to the rate of photosynthesis (Schwendenmann *et al.*, 2006; Konnerup *et al.*, 2007). Hence, if net primary production (NPP) increases, the extent to which plants influence CO₂ and CH₄ production in peatlands is also likely to increase, potentially increasing the release of these gases to the atmosphere. Plants growing in tropical peatlands are likely to have a higher NPP during the dry season than the wet season due to a combination of decreased cloud cover and increased solar radiation, lower wind speed and higher air temperatures (Nemry *et al.*, 1999; Schuur, 2003; Mohamed *et al.*, 2004). Although in peatlands with substantial water table drawdown, water stress may result in decreased NPP. The

temporal trends for CO₂ and CH₄ fluxes found in previous studies of tropical peatlands indicate a strong seasonal (wet and dry) influence on their magnitude, with CO₂ fluxes being greater during the dry season and lower during the wet season (Jauhiainen *et al.*, 2005; Schedkbauer *et al.*, 2010); the reverse applied to CH₄ fluxes (Biswas *et al.*, 2007; Grand and Gaidos, 2010). This was particularly evident in tropical peatlands which exhibited pronounced drawdown of the water table during the dry season compared to those which were inundated throughout the annual cycle.

As noted previously, CO₂ and CH₄ fluxes from peatland systems may be affected by various controlling factors, resulting in strong temporal variability. It is important to understand how these fluxes vary with changing environmental conditions over both long and short time scales to provide accurate representations of the controlling mechanisms within tropical peatlands for use in modelling and estimation of future CO₂ and CH₄ fluxes under different climatic scenarios. In the Neotropics, CO₂ and CH₄ fluxes from peat surfaces have been found to vary substantially depending on the dominant vegetation community present (Sjogersten *et al.*, 2010; Wright *et al.*, 2011). This is likely to result partly from the influence of vegetation on environmental factors affecting fluxes and also from direct plant influences on system functions (e.g. root exudates, peat aeration *etc.*). However, the extent of the temporal variation between different vegetation communities is still not well understood.

The objectives of the present study were to determine:

- i) whether CO₂ and CH₄ fluxes show intra-annual variation in a Neotropical peatland
- ii) the extent of any inter-annual variation in CO₂ and CH₄ fluxes
- iii) whether CO₂ and CH₄ fluxes follow a circadian rhythm

5.2 Materials and Methods

Three sites with differing dominant vegetation communities within the San San Pond Sak peatland, namely *R. taedigera*, *C. panamensis* and *Cyperus* sp., were sampled to assess the variation in CO₂ and CH₄ fluxes on a diurnal, intra-annual and inter-annual basis.

5.2.1 Variation in intra-annual fluxes

At each site, five 2 m x 2 m plots were established separated by a distance of at least 20 m; each plot was further divided into two subplots. Samples of peat surface gas flux were taken from each subplot on the 21st (*Cyperus* sp. and *C. panamensis* sites) and 22nd (*R. taedigera* site) day of each month between February-November 2007, excluding October. The sampling locations were randomly selected and all vegetation, fallen branches and emerging seedlings were removed from the plots before commencing gas flux measurements.

Gas samples were taken using a headspace with a volume of 7.8 dm³ and followed the sampling protocol outlined in Section 3.2.1. The gas samples were transported to Nottingham where they were analysed by gas chromatography (GC 2014, Shimadzu, Milton Keynes, UK) using a 1 ml sampling loop and a molecular sieve column; detection of CO₂ was by thermal conductivity and CH₄ by flame ionisation.

5.2.2 Diurnal variation in gas fluxes

To quantify the diurnal patterns of CO₂ and CH₄ fluxes, five 1 x 1 m plots were established at all sites, separated by a distance of at least 5 m. Samples were taken in February 2009 at the *Cyperus* sp. site only and during August 2009 for all three sites. Sampling began in the afternoon of Day 1 and carried on into Day 2, with the samples being collected at 1600, 1830, 2200, 0730, 0930 and 1300 h local time. The 1830 and 0730 h time points were respectively soon after sunset and sunrise.

Samples were collected using a 384.8 cm³ headspace following the protocol outlined in Section 3.2.1 and shipped to Nottingham for analysis as described in Section 3.2.2.

5.2.3 Comparison of gas fluxes in July and August 2007 and 2009

Measurements were made in July and August 2007 and 2009 to investigate inter-annual variation in CO₂ and CH₄ fluxes. The 2007 samples were those used in the study of intra-annual fluxes carried out in 2007, and were collected and processed as described in Section 5.2.1. The 2009 samples were collected from the same sample plots as in 2007 using a 384.8 cm³ headspace and the sampling and analysis protocols described in Section 3.2.1.

5.2.4 Measurements of rainfall and air and soil temperature

Data for rainfall, air temperature and solar radiation were sourced from the weather station at the Smithsonian Research Institute on Isla Colon. Environmental conditions were recorded at 15 minute intervals using a rain gauge (CS700, Campbell Scientific Inc, Utah, USA), temperature and relative humidity probe (CS215, Campbell Scientific Inc, Utah, USA) and a pyranometer (L1200X, Campbell Scientific Inc, Utah, USA). In conjunction with the intra- and inter-annual measurements of gas fluxes, peat temperature was measured at 10 cm depth in each plot at the time of gas sampling. To enable comparison between the gas flux and meteorological data, the data from the monitoring station were processed to obtain hourly mean temperature at the time of sampling and mean air temperature for the 24 h period preceding sampling. The rainfall data were used to calculate cumulative rainfall for the 24 h, 1 week and 1 month periods preceding each gas sampling event. The solar radiation data were used to calculate the mean radiation at the time of sampling.

5.2.5 Data analysis

All CO₂ and CH₄ fluxes were tested for normality and a Shapiro-Wilk's test was used with a significance value of $p < 0.01$. If the null hypotheses were rejected the data was transformed to meet the assumptions of normality. Annual CO₂ fluxes were square-rooted and CH₄ fluxes had 1 added to ensure they were all positive values and then log₁₀ transformed. The diurnal CO₂ fluxes met the assumption of normality except for the *C. panamensis* site, for which the values were square rooted. All diurnal CH₄ fluxes were transformed and those for the *R. taedigera* and *C. panamensis* sites had 2 added to the values to ensure that all were positive before being transformed using log_e. Fluxes for the *Cyperus* sp. site in February and August had 1 added before being transformed using an inverse double log. When comparing the fluxes for 2007 and 2009, the values were all transformed using log₁₀.

Intra-annual fluxes were analysed on a plot basis (each set of subplots was averaged to produce a single measurement for each plot) using a repeated measures analysis of variance (ANOVA), with site, time and their interactions as fixed effects; plot was used as a blocking term. The relationships between gas fluxes and environmental conditions for each measurement date were analysed by regression analysis. Diurnal fluxes were analysed using repeated measures ANOVAs for each site, with plot as a blocking term and time as the fixed effect. The relationship between gas fluxes and environmental conditions for each site and time were analysed by regression analysis.

The fluxes in July and August 2007 and 2009 were compared using a general ANOVA, with site, time and their interactions as fixed effects; plot was used as a blocking term. The influence of cumulative rainfall during the 24 h and 28 d periods preceding each sampling event on CO₂ and CH₄ fluxes was tested by linear regression analysis. Relationships between

gas fluxes and environmental conditions for each measurement date were analysed by regression analysis.

All statistical analyses were performed using Genstat version 11 (Lawes Agricultural Trust, Rothamsted Experimental Station).

5.3 Results

5.3.1 Variation in intra-annual fluxes

5.3.1.1 CO₂ fluxes

All sites showed a decline in CO₂ flux from the maximum values recorded in February and March to a minimum in June and July; this was followed by an increase during the remainder of the observation period. The greatest overall CO₂ flux of 402.1 mg m⁻² h⁻¹ was found at the *C. panamensis* site in February 2007. Excluding the measurements made in November 2007, the greatest monthly flux was consistently found at the *C. panamensis* site, followed by the *R. taedigera* and *Cyperus* sp. sites, but the site differences were less pronounced in June and July when fluxes were low. There were no obvious differences in the inter-site variation in CO₂ fluxes depending on whether these were expressed as mean or median values (Fig. 5.1). Fluxes at the *R. taedigera* site ranged from 74 to 352 mg CO₂ m⁻² h⁻¹, while those for the *C. panamensis* and *Cyperus* sp. sites ranged from 132 to 402 mg CO₂ m⁻² h⁻¹ and 59 to 294 mg CO₂ m⁻² h⁻¹ respectively based on monthly mean values.

Mean values for solar radiation and air temperature for the periods when gas fluxes were measured (Figs. 5.2, 5.3) revealed a significant effect of solar radiation on CO₂ fluxes, with a general increase in CO₂ efflux with increasing solar radiation receipts (Fig. 5.4). There was no significant effect of temperature ($F_{1,129}=0.22$, $p=0.6$). Similarly, no significant effect

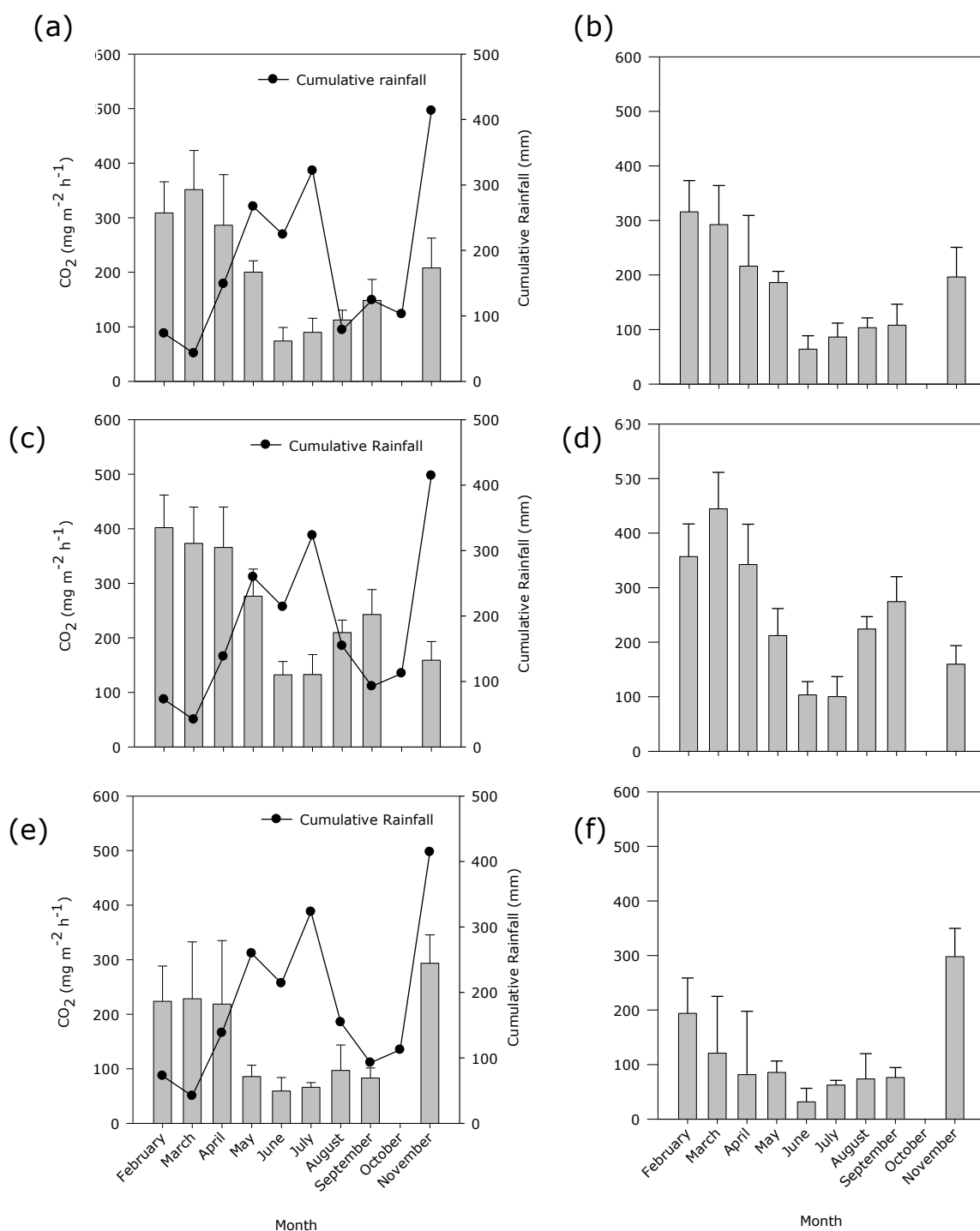


Figure 5.1. Mean CO₂ fluxes and cumulative rainfall during the 28 d period preceding each sampling event between February and November 2007 (excluding October) for a) *R. taedigera*, c) *C. panamensis* and e) *Cyperus* sp. and median CO₂ fluxes for b) *R. taedigera*, d) *C. panamensis* and f) *Cyperus* sp. Single standard errors of the mean (n=5) are shown for CO₂ fluxes. Regression analysis of the effect of rainfall for all sites: $F_{1,129}=12.84$, $p<0.001$. Repeated measures ANOVA summary:
Time: $F_{8,129}=12.28$, $p<0.001$
Site: $F_{2,129}=3.97$, $p<0.05$
Time*Site: $F_{16,129}=1.44$, $p=0.2$

on CO₂ fluxes was found either for short term variation in rainfall (i.e. total during the 24 h period preceding gas sampling; $F_{1,129}=0.63$, $p=0.4$) or air temperature at time of sampling ($F_{1,129}=0.22$, $p=0.9$). However, there was a highly significant effect of monthly rainfall on CO₂ fluxes as these were quadratically correlated with rainfall (Fig. 5.5); thus, months when CO₂ fluxes were lowest for all sites (June and July) corresponded to periods when cumulative rainfall was greatest (Fig. 5.1). In 2007, rainfall was lowest in February and March (73 and 42.5 mm, respectively, Table 5.1), but increased to 322.5 mm during July. Monthly rainfall then decreased to between 78 and 154 mm in August, September and October

2007. Rainfall was greatest in November (413.5 mm). Cumulative rainfall in 2007 during February, March and August was substantially lower than for the equivalent periods in 2006, 2008 and 2009. Cumulative rainfall in November 2007 was substantially greater than in the two preceding years but similar to that in 2008.

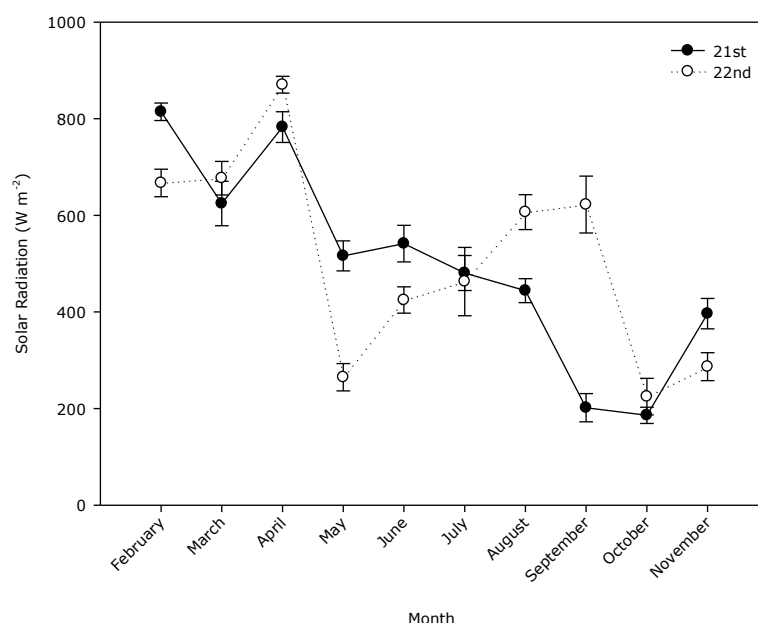


Figure 5.2. Mean solar radiation between 1000 and 1500 h \pm SEM (n=21) on the 21st (*Cyperus* sp. and *C. panamensis* sampling day) and 22nd (*R. taedigera* sampling day) of each month.

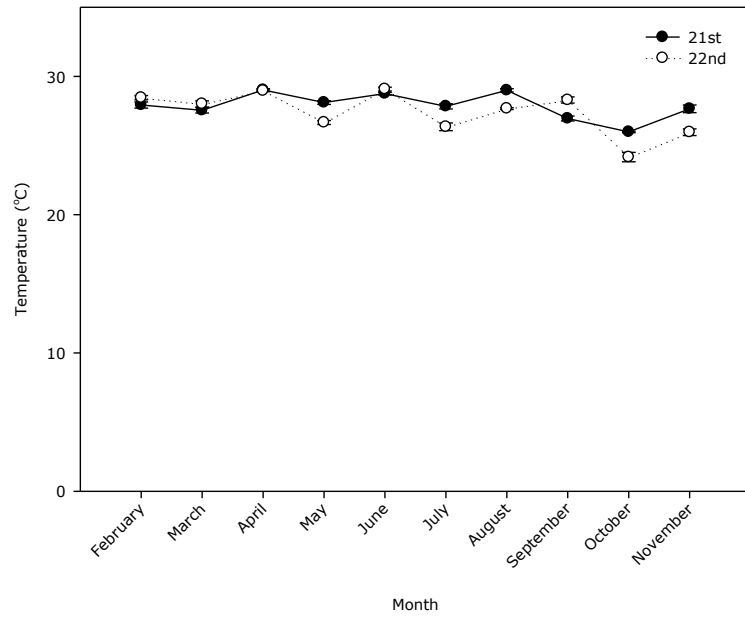


Figure 5.3. Mean air temperature \pm SEM ($n = 21$) between 1000 and 1500 h on the 21st (*Cyperus* sp. and *C. panamensis* sampling day) and 22nd (*R. taedigera* sampling day) of each month.

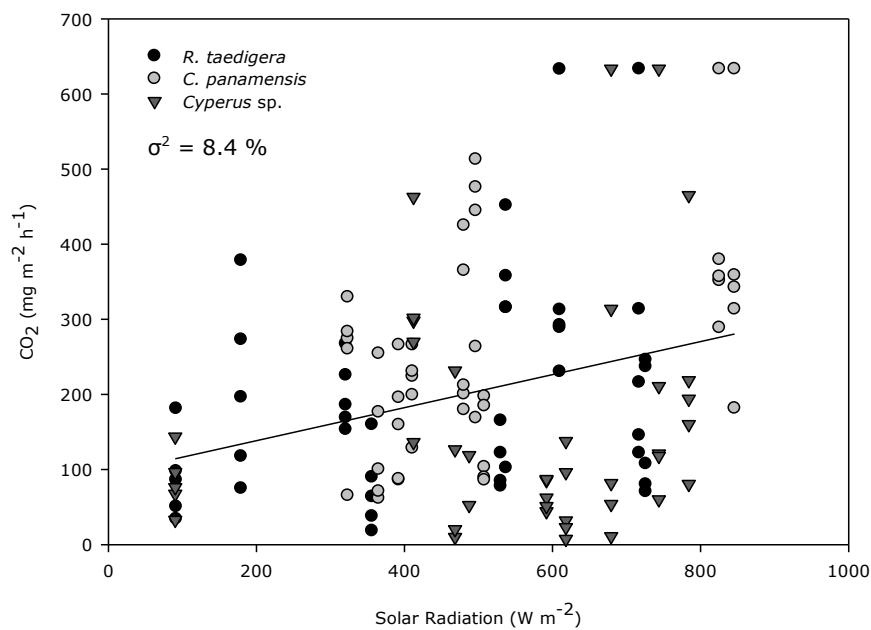


Figure 5.4. Correlation between CO₂ efflux and solar radiation; linear regression is shown. Regression analysis: $F_{1,129} = 12.75$, $p < 0.001$.

Table 5.1. Cumulative monthly rainfall (mm) for 2005-2009 representing the equivalent 28 d period preceding gas flux measurements in 2007: A) 28 d period preceding the 21st day of each month, when the *C. panamensis* and *Cyperus* sp. sites were sampled; B) 28 d period preceding the 22nd day of each month, when the *R. taedigera* site was sampled. These datasets show that temporal variation in rainfall was substantial even over these slightly different timescales. Extremely high or low rainfall values are highlighted in bold.

	2005		2006		2007		2008		2009	
	A	B	A	B	A	B	A	B	A	B
January	-	-	264	264	356	314	400	319	264	237
February	-	-	238	234	73	73	224	212	706	676
March	-	-	155	223	43	42	85	86	467	468
April	-	-	312	312	149	138	192	175	92	108
May	-	-	163	144	267	260	134	170	515	510
June	-	-	142	142	224	214	142	142	96	96
July	195	198	322	341	322	323	279	274	268	268
August	618	618	346	293	78	154	299	287	369	358
September	203	197	189	179	124	93	107	80	190	188
October	127	123	188	165	103	112	167	173	285	285
November	281	251	203	219	413	414	492	664	-	-
December	167	153	301	300	253	268	442	208	-	-

5.3.1.2 2 CH₄ fluxes

No significant effects of site, time or site*time interaction were found for CH₄ fluxes (Fig. 5.6). These ranged from 0.12 to 12.63 mg CH₄ m⁻² h⁻¹ at the *R. taedigera* site, -0.88 to 0.54 mg CH₄ m⁻² h⁻¹ at the *C. panamensis* site and 1.06 to 1.82 mg CH₄ m⁻² h⁻¹ at the *Cyperus* sp. site. No significant effects of cumulative rainfall during the 28 d or 24 h periods preceding CH₄ flux measurements ($F_{1,133}=0.44$, $p=0.5$; $F_{1,133}=0.01$, $p=0.9$), air temperature at the time of sampling ($F_{1,133}=1.37$, $p=0.2$) or solar radiation at the time of sampling ($F_{1,133}=0.02$, $p=0.9$) were detected. The two highest mean CH₄ effluxes recorded in 2007 were at the *R. taedigera* site (7.0 ± 6.37 mg CH₄ m⁻² h⁻¹ in February and 12.6 ± 14.36 mg CH₄ m⁻² h⁻¹ in September) and this site also showed the greatest variability (Fig. 5.6a).

CH₄ uptake by the peat was observed at the *C. panamensis* site during August, September and November (0.62 ± 0.28 , 0.88 ± 0.67 and 0.28 ± 0.42 mg CH₄ m⁻²

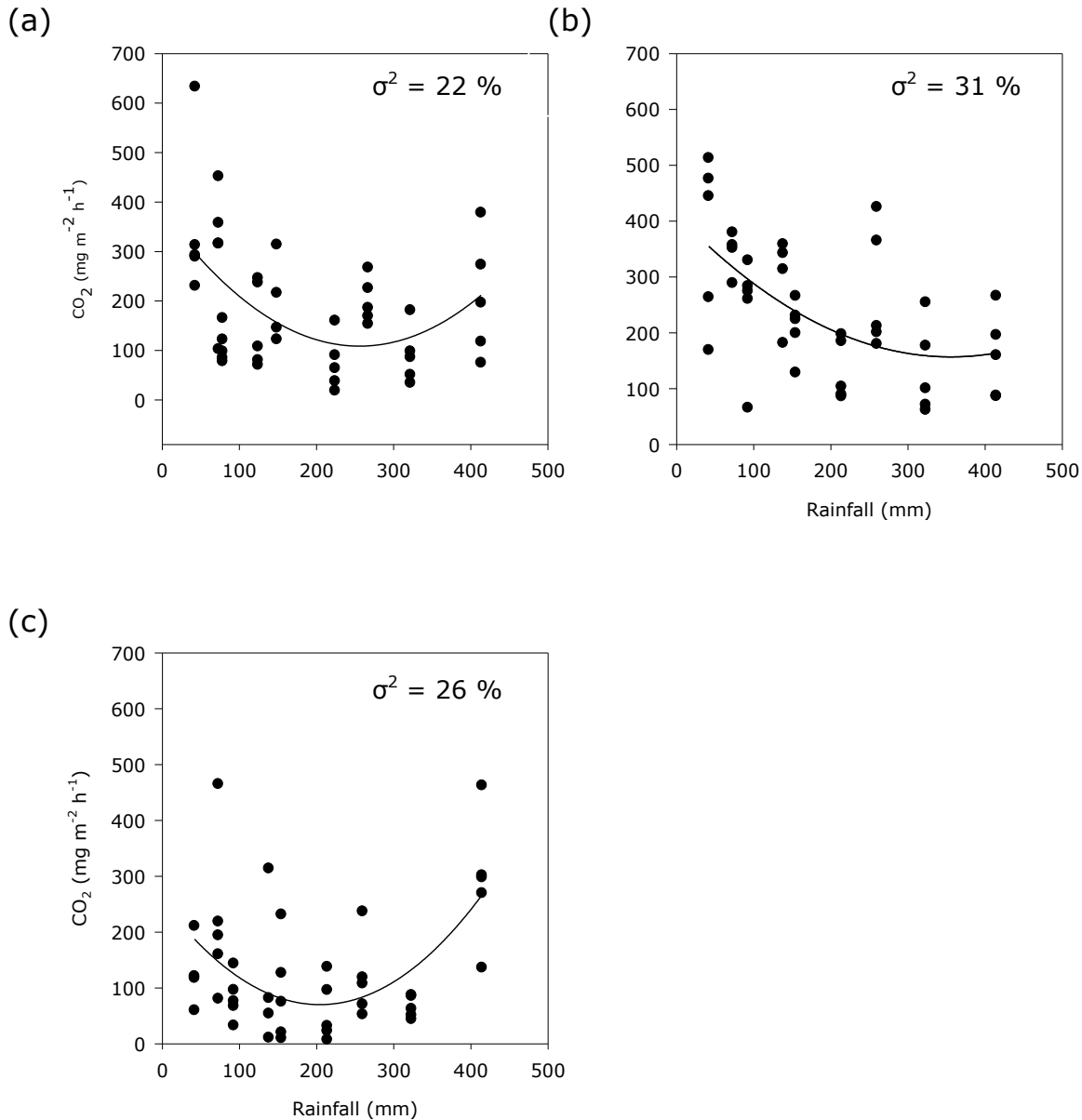


Figure 5.5. Correlation between CO₂ flux and cumulative rainfall during the preceding 28 d period in 2007 for a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. Polynomial regressions and the variance accounted for are shown. Polynomial regression analysis summary:

- a) $F_{2,43} = 7.11$, $p = 0.002$
- b) $F_{2,42} = 10.32$, $p < 0.001$
- c) $F_{2,42} = 8.44$, $p < 0.001$

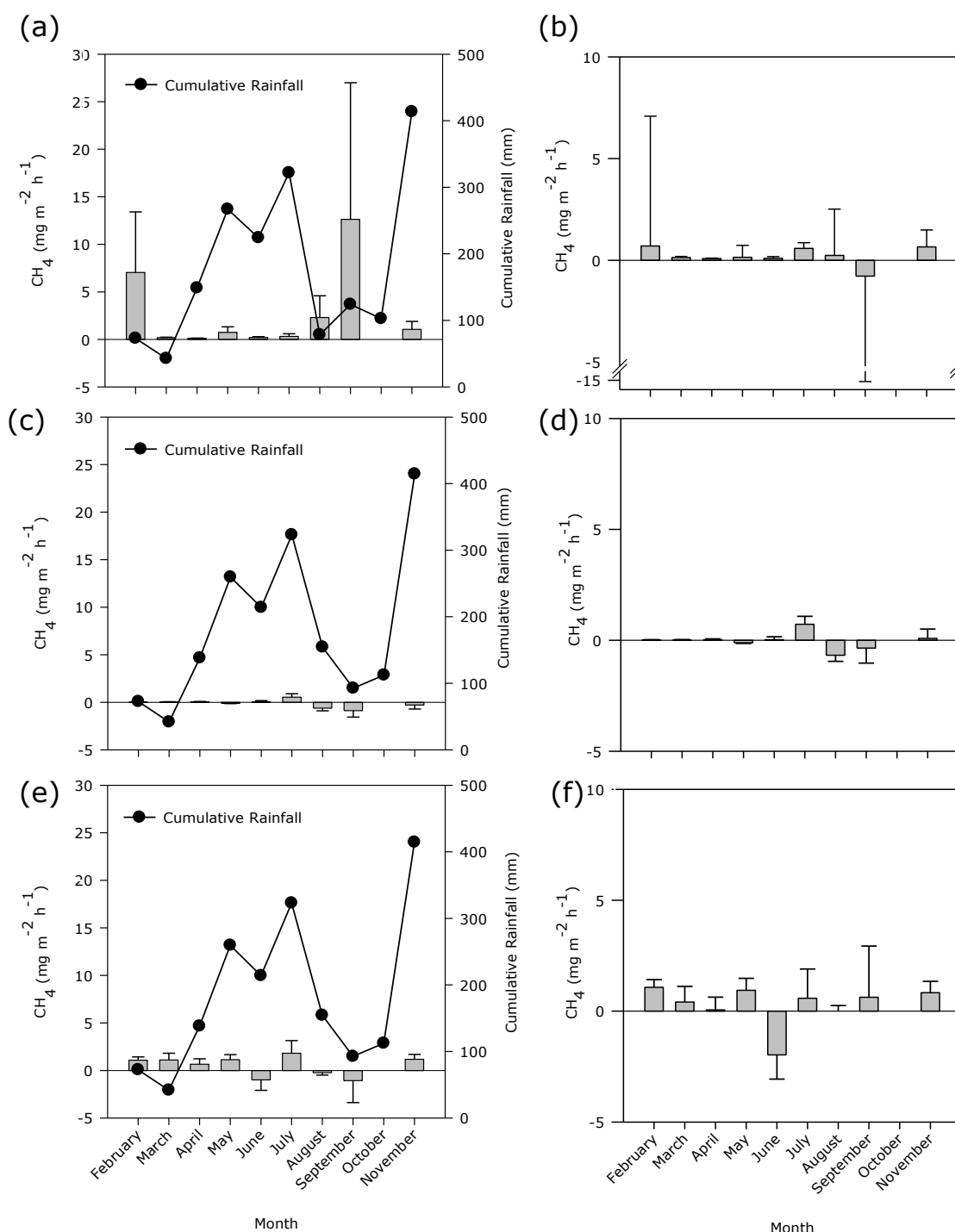


Figure 5.6. Mean CH₄ fluxes and cumulative rainfall during the 28 d period preceding each sampling event between February and November 2007 (excluding October) for a) *R. taedigera*, c) *C. panamensis* and e) *Cyperus* sp. and median CH₄ fluxes for b) *R. taedigera*, d) *C. panamensis* and f) *Cyperus* sp. Single standard errors of the mean (n=5) are shown for CH₄ fluxes. Repeated measures ANOVA summary:

Time: $F_{8,133} = 0.57$, $p = 0.5$

Site: $F_{2,133} = 0.89$, $p = 0.4$

Time*Site: $F_{16,133} = 0.92$, $p = 0.4$

h^{-1} , respectively; Fig. 5.6c). CH_4 uptake was also observed at the *Cyperus* sp. site in June and September (0.99 ± 1.09 and 1.06 ± 2.31 $\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ respectively (Fig. 5.6e).

When comparing the mean and median CH_4 fluxes, the only distinct difference in the pattern of results was at the *R. taedigera* site, where the high fluxes seen in February and September when mean values are considered (Fig. 5.6a) were not reflected by the median values (Fig. 5.6b); instead, there was a small efflux in all months except September when a small uptake of CH_4 occurred, reflecting a limited number of very high measured CH_4 fluxes at this site.

5.3.2 Diurnal variation in gas fluxes

5.3.2.1 CO_2 fluxes

No significant diurnal variation in CO_2 flux was detected for the *R. taedigera* site (Fig. 5.7a), but significant diurnal variation was found at the *C. panamensis* and *Cyperus* sp. sites (Fig. 5.7b, c). Fluxes at the *R. taedigera* site varied between 271 and 355 $\text{mg m}^{-2} \text{ h}^{-1}$, while those at the *C. panamensis* site ranged between 229 and 597 $\text{mg m}^{-2} \text{ h}^{-1}$; CO_2 flux at the *C. panamensis* site was greatest at 1600 h and lowest at 0730 h, with a gradual increase between 0730 and 1600 h. CO_2 fluxes at the *Cyperus* sp. site followed a similar diurnal pattern to the *C. panamensis* site, ranging from a maximum of 525 $\text{mg m}^{-2} \text{ h}^{-1}$ at 1600 h to a minimum of 159 $\text{mg m}^{-2} \text{ h}^{-1}$ at 0730 h.

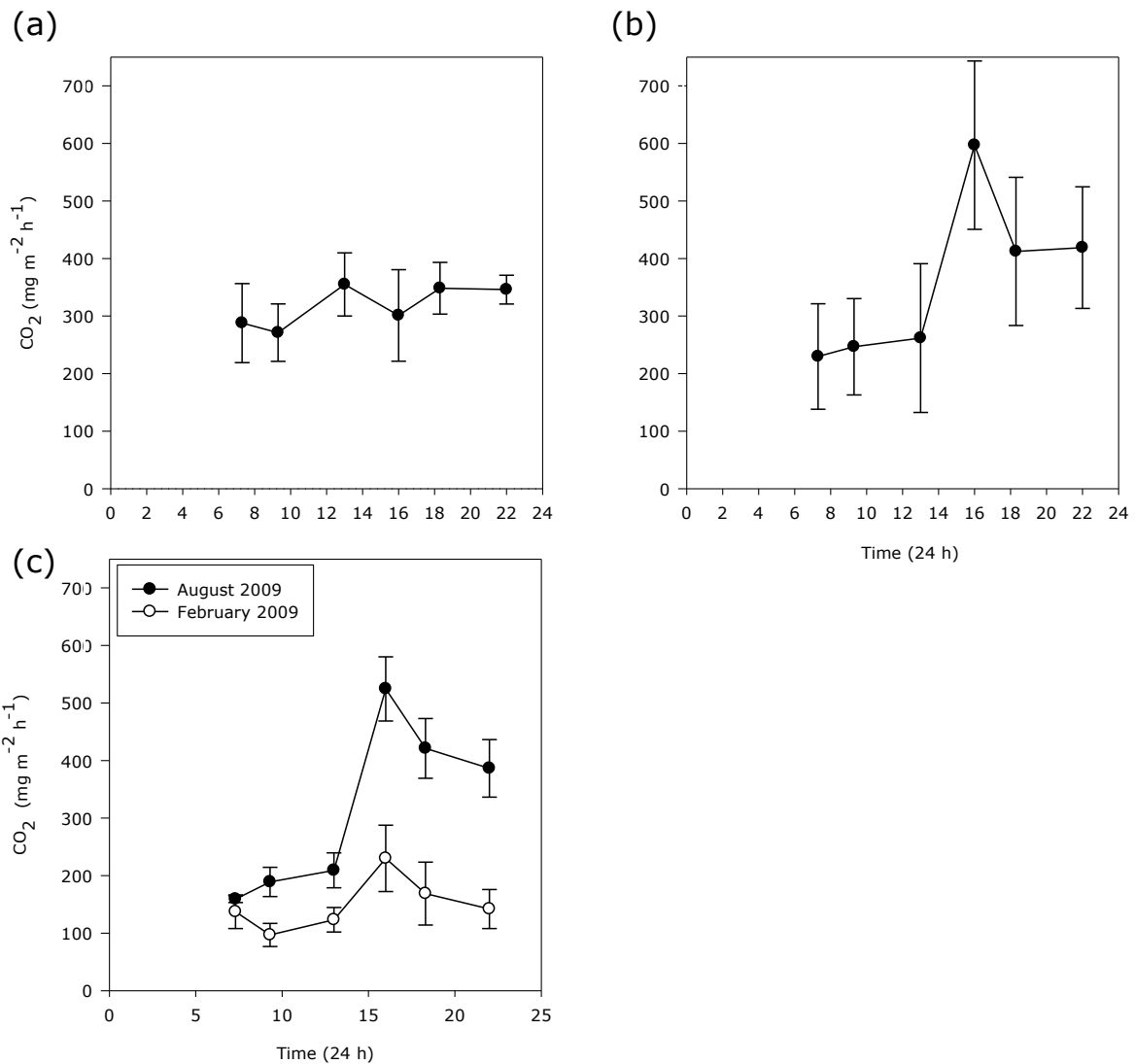


Figure 5.7 Diurnal CO₂ fluxes in August 2009 for the a) *R. taedigera* and b) *C. panamensis* sites; (c) CO₂ fluxes from c) *Cyperus* sp. site in February and August 2007. Double standard errors of the mean are shown (n=5). Repeated measures ANOVA summary:

- a) $F_{5,25} = 0.90$, $p = 0.4$
- b) $F_{5,28} = 7.34$, $p < 0.05$
- c) August: $F_{5,28} = 24.92$, $p < 0.001$
 February: $F_{5,29} = 1.44$, $p = 0.3$
 Month: $F_{1,59} = 165.52$, $p < 0.001$

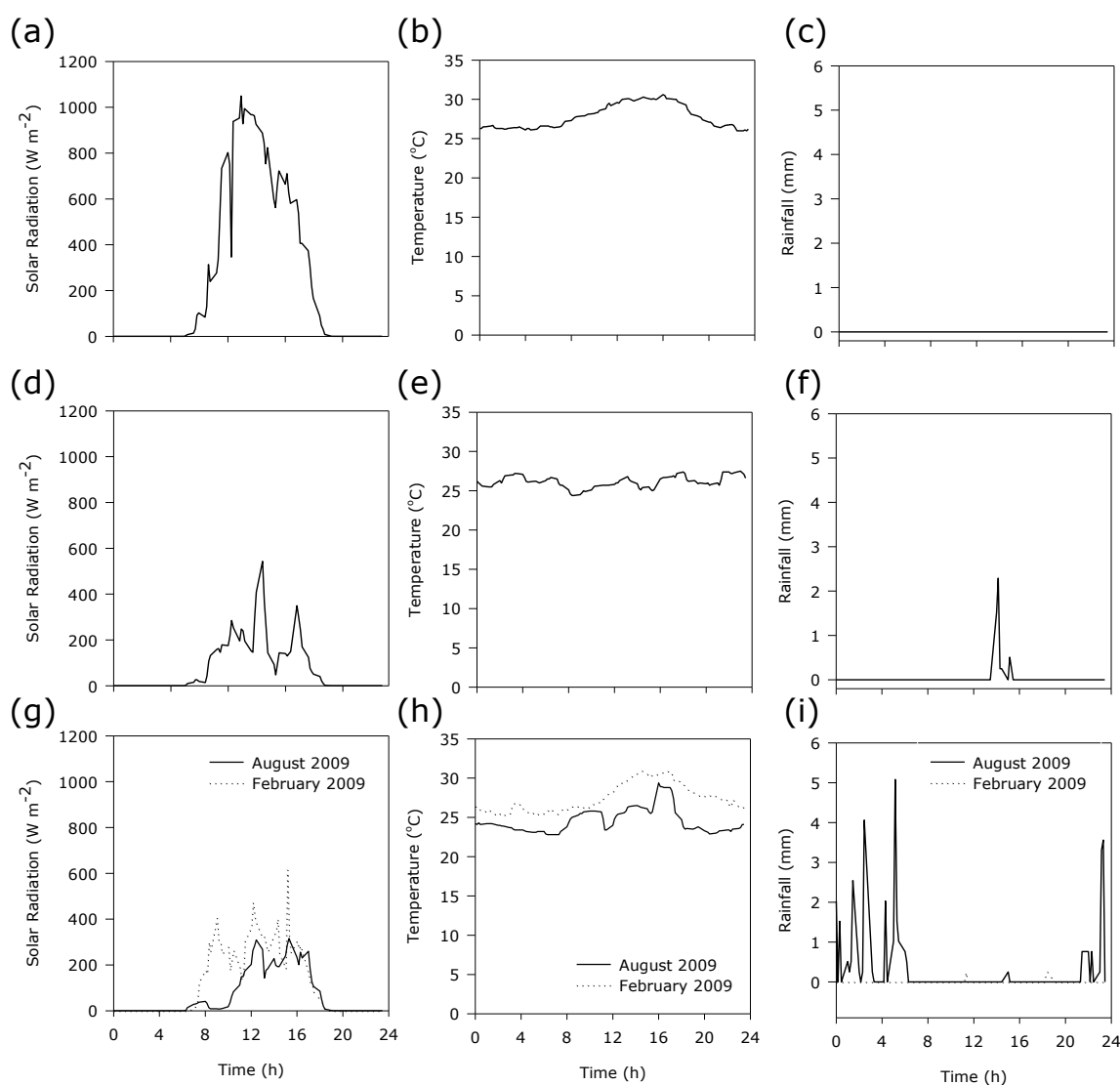


Figure 5.8. Diurnal timecourses of solar radiation, air temperature and rainfall constructed from measurements made at 15 min intervals during the 24 h of surface gas flux sampling periods for a), b) and c) *R. taedigera*, d), e) and f) *C. panamensis* and g), h) and i) *Cyperus* sp. in February and August 2009.

The timecourses of CO_2 fluxes at the *Cyperus* sp. site in February 2009 were similar to those observed in August 2009 (Fig. 5.7c). There was a significant diurnal variation in CO_2 flux and the trends in both months followed a similar pattern to that obtained for the *C. panamensis* site in August. The CO_2 fluxes in February were lower than those observed in August ($p < 0.001$; Fig. 5.7c), with a difference of $300 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ between the peak values recorded at 1600 h. Fluxes at 0730 h were similar in February and August (137 ± 29 and $159 \pm 6 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$,

respectively). There was no detectable month*time interaction ($p=0.9$). In this context, it is worth noting that rainfall in August 2009 was over six times greater than in February 2009 (Table 5.1).

There was an overall effect of air temperature as CO_2 flux was positively correlated with temperature (Fig. 5.9), but there was no significant effect of solar radiation on the diurnal timecourse of CO_2 fluxes ($F_{1,113} = 11.42$, $p=0.8$; Fig. 5.8). There was no significant effect of rainfall at time of sampling on CO_2 effluxes ($F_{1,113} = 0.13$, $p=0.7$; Fig. 5.8).

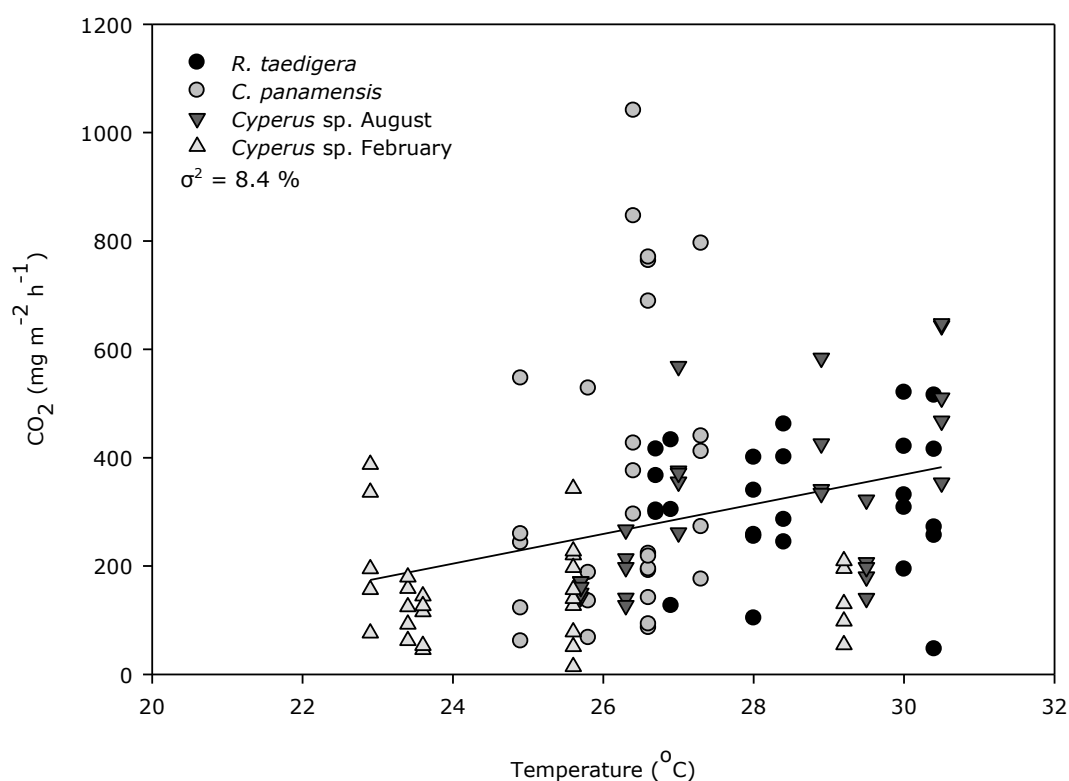


Figure 5.9. Correlation between CO_2 flux and air temperature at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites. The fitted linear regression and variance² are shown. Linear regression: $F_{1,113} = 11.42$, $p=0.001$.

5.3.2.2 CH_4 fluxes

No significant diurnal variation in CH_4 fluxes was found at any of the sites examined (Fig. 5.10a-c). CH_4 fluxes at the *Cyperus* sp. site were generally lower than at the other sites and invariably close to zero, with a

small peak of $0.61 \pm 0.58 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at 1300 h. At the *C. panamensis* site, CH_4 fluxes were lowest between 0730 and 1300 h, after which there was a general increase to a peak of $2.62 \pm 1.9 \text{ mg m}^{-2} \text{ h}^{-1}$ at 2200 h. Fluxes at the *R. taedigera* site were consistently greater than at the other two sites, with only a single value at 1600 h being $<1 \text{ mg m}^{-2} \text{ h}^{-1}$; all other values were between 1–3 $\text{mg m}^{-2} \text{ h}^{-1}$.

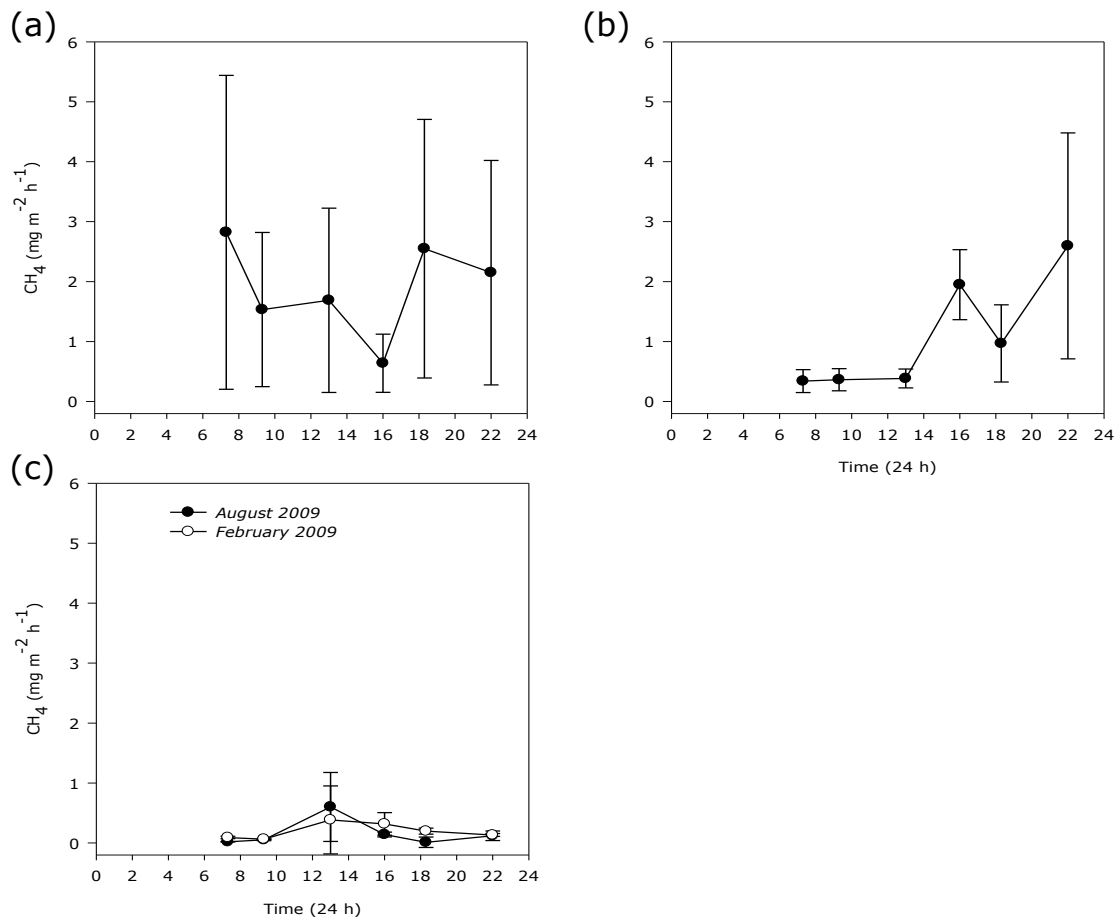


Figure 5.10. Diurnal timecourses of CH_4 fluxes in August 2009 for the a) *R. taedigera* and b) *C. panamensis* sites; c) CH_4 fluxes from *Cyperus sp.* site in February and August 2007. Double standard errors of the mean are shown (n=5). Repeated measures ANOVA summary:

- a) $F_{5,29}=0.52$, $p=0.7$.
- b) $F_{5,28}=2.57$, $p=0.2$.
- c) August: $F_{5,29}=1.14$, $p=0.4$.
- February: $F_{5,29}=1.44$, $p=0.3$
- Month: $F_{5,59}=0.49$, $p=0.6$

Figure 5.10c also shows diurnal CH_4 fluxes at the *Cyperus sp.* site in February 2009. The values were generally lower than in August 2009 and $<0.1 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ except at 1830 h (February), when the peak CH_4

efflux of $0.12 \pm 0.05 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ was recorded. The peak value in February occurred later in the day (1830 h) than in August (1300 h; Fig. 5.10c). There were no significant effects of solar radiation ($F_{1,118} = 0.02$, $p=0.9$), air temperature ($F_{1,118} = 1.24$, $p=0.3$) or rainfall ($F_{1,118} = 0.85$, $p=0.4$) at the time of sampling on CH_4 fluxes (Fig. 5.8).

5.3.3 Comparison of gas fluxes in July and August 2007 and 2009

5.3.3.1 CO₂ fluxes in July and August 2007 and 2009

CO_2 fluxes were greater in both July and August 2009 than the corresponding values in 2007 ($p < 0.001$; Fig. 5.11). For example, in July 2009, the CO_2 flux from the *R. taedigera* site ($431 \text{ mg m}^{-2} \text{ h}^{-1}$) was over four times greater than that recorded at the same site in July 2007, illustrating the substantial temporal differences within these sites. No significant differences between sites were detected over the time period examined.

A significant positive correlation between CO_2 flux and cumulative rainfall over the preceding month was also found (Fig. 5.12a). Cumulative rainfall data for these time periods are shown in Table 5.1. There were no significant effects of solar radiation ($F_{1,46}=2.86$, $p=0.1$) or temperature ($F_{1,46}=2.37$, $p=0.1$) at the time of sampling on CO_2 fluxes.

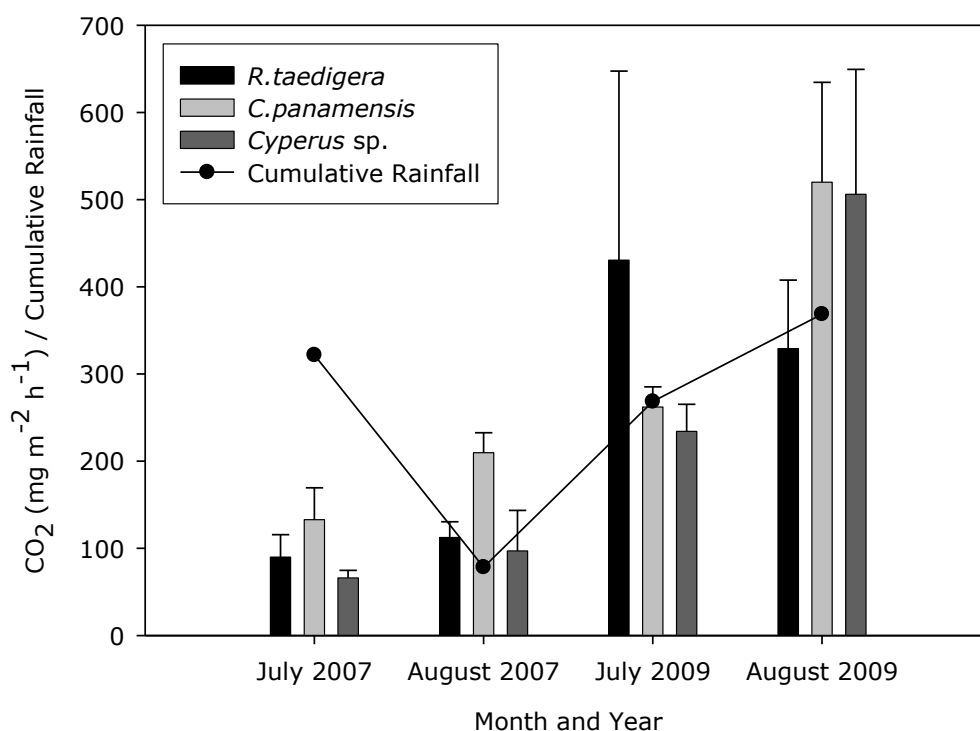


Figure 5.11. CO₂ fluxes for all sites in July and August 2007 and 2009 and cumulative rainfall during the preceding 28 days. Single standard errors of the mean are shown (n=5). ANOVA summary:

Site: $F_{2,46} = 1.32$, $p = 0.3$
 Year: $F_{1,46} = 31.31$, $p < 0.001$
 Site*Year: $F_{2,46} = 2.46$, $p = 0.1$

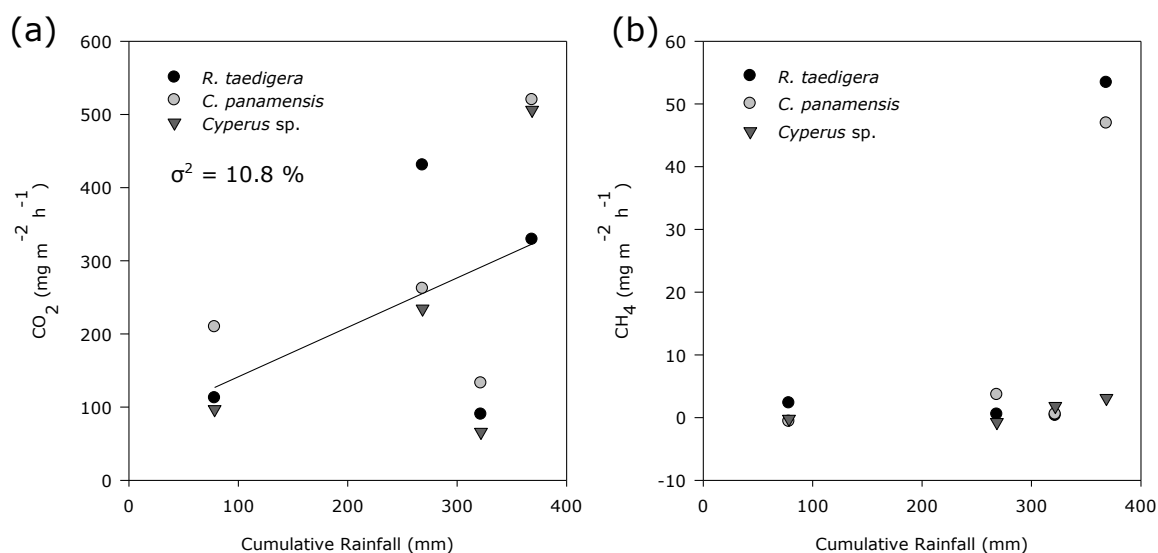


Figure 5.12. Relationship between a) CO₂ and b) CH₄ fluxes and cumulative rainfall during the preceding 28 d period. The fitted linear regression is shown for CO₂. Regression analysis:

a) $F_{1,46} = 6.58$, $p < 0.05$
 b) $F_{1,49} = 2.35$, $p = 0.1$

5.3.3.1 CH₄ fluxes in July and August 2007 and 2009

There was a significant variation between sites in CH₄ flux, which was generally greatest at the *R. taedigera* site, where there were no months of recorded uptake, followed by the *C. panamensis* site, where a small CH₄ uptake was recorded in August 2007, and finally the *Cyperus* sp. site, where small effluxes (<4 mg CH₄ m⁻² h⁻¹) were found in July 2007 and August 2009. Uptake occurred in August 2007 and July 2009 (Fig. 5.13).

There was a significant effect of measurement date on CH₄ flux in both years (Fig. 5.13). CH₄ fluxes were greatest at the *R. taedigera* and *C. panamensis* sites in August 2009 (53.4 and 46.9 mg m⁻² h⁻¹, respectively), when the values were approximately 10-fold greater than for the other sampling dates. Net CH₄ uptake was observed at the *C. panamensis* site in August 2007 (0.62±0.28 mg CH₄ m⁻² h⁻¹) and at the *Cyperus* sp. site in July 2009 (0.74±0.40 mg CH₄ m⁻² h⁻¹), illustrating a rapid switch from net uptake to net production between July and August 2009. No correlation was found between CH₄ flux and cumulative rainfall during the preceding 28 d (Fig. 5.11b) or 24 h ($p>0.05$). There were no significant effects of solar radiation ($F_{1,49}=2.39$, $p=0.1$) and air temperature ($F_{1,49}=2.31$, $p=0.1$) at the time of sampling on CH₄ fluxes.

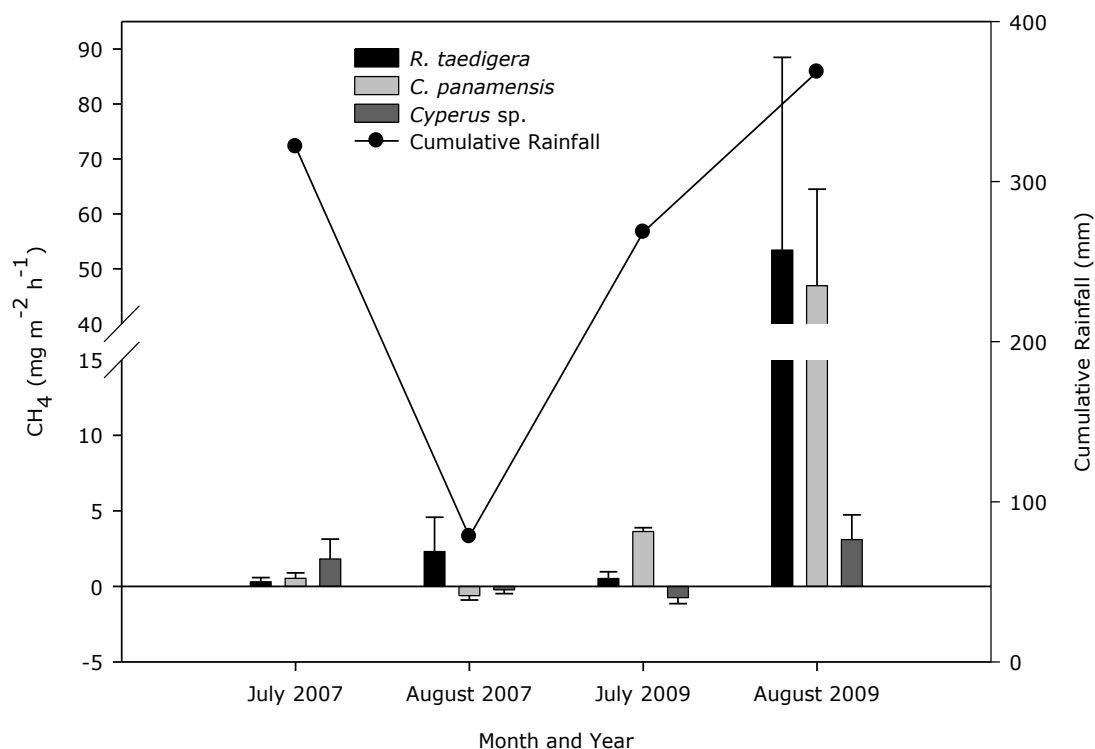


Figure 5.13. CH₄ fluxes for all sites in July and August 2007 and July and August 2009. Single standard errors of the mean are shown (n=5). ANOVA summary:

Site:	$F_{2,47} = 7.51, p < 0.05$
Year:	$F_{1,47} = 14.15, p < 0.001$
Site*Year:	$F_{2,47} = 11.40, p < 0.001$

5.4 Discussion

5.4.1 Annual variation in fluxes

The CO₂ effluxes measured in the San San Pond Sak peatland were comparable to those obtained for other tropical peatland systems (Table 2.1). In general, CO₂ flux varied as expected during the annual cycle, being higher during the drier months and lower during the wetter months (Fig. 5.1). Previous studies have shown that CO₂ production in peatlands generally increases when the water table falls below the peat surface

(Updegraff *et al.*, 1995; Jauhianen *et al.*, 2005; Hirano *et al.*, 2009; Schedlbauer *et al.*, 2009). The exact height of the water table when the measurements were made in the present study was not recorded, but cumulative monthly rainfall provides an indication of when the system is likely to have been saturated. From this information we can extrapolate; thus, knowing that CO₂ production is generally greater during months of lower rainfall, it is likely that the surface layer of the peat profile was more aerated during these periods, thereby increasing aerobic respiration. It should also be noted that several studies have highlighted the importance of microtopography and the presence of hummocks and hollows at many peatland sites (Jauhiainen *et al.*, 2005).

CO₂ flux was found to vary between sites (Fig. 5.1). Although the patterns of CO₂ efflux across the year were similar for each site (i.e. higher efflux during the dry season and lower during the wet season), the magnitude and range of fluxes varied between sites, perhaps because of the differing dominant vegetation species, particularly as autotrophic respiration by roots and from peat oxidation (heterotrophic respiration) were not separated. The contribution of root respiration to surface CO₂ fluxes is known to vary depending on the species involved (Whiting and Chanton, 1993; Thomas *et al.*, 1996; Crow and Wieder, 2005). Root exudates, in combination with the circadian rhythm of root respiration, may increase CO₂ evolution from roots and the surrounding substrate, particularly if exudate release coincides with optimum conditions for respiration as this has the potential to induce peaks in the rate of CO₂ evolution. The differences in dominant vegetation between sampling sites are therefore likely to have influenced respiration within the roots and in the surrounding peat. CO₂ fluxes were lowest at the *Cyperus* sp. site (Fig. 5.1e). *Cyperus* sp. has a relatively shallow rooting system compared to *R. taedigera* and *C. panamensis*, potentially impacting on both aeration and release of root exudates, restricting both to the rooting zone within the uppermost 65 cm of the peat profile (*cf.* Section 6.3; Wright *et al.*,

2011). The total root biomass as well as the depth of the rooting zone will potentially affect fluxes, as the greater the rooting biomass then the greater the potential contribution from autotrophic respiration and the greater the potential exudate input. In general, CO₂ effluxes were greatest at the *C. panamensis* site (Fig. 5.1c). *C. panamensis* is a tree species which consistently had relatively low root biomass to depths of c. 110 cm (*cf.* Section 6.3), although it should be noted that large roots were avoided during sampling due to the inability of the corer to sever them. It is therefore likely that the true root biomass was greater than that recorded and hence may have had a greater impact on fluxes than is apparent from this study (Li *et al.*, 2004). The significant effect of solar radiation on CO₂ fluxes (Fig. 5.4) can also be linked to the influence of the surface vegetation. When there is increased solar radiation the vegetation receives increased quantities of PAR, increasing photosynthesis and hence the quantity of photoassimilates produced and released to the peat (Yang and Cai., 2006). As all the vegetation species in this investigation are C3 species they will all have the same light response curve.

The intra-annual variation in CH₄ fluxes at the three sites examined showed no clear temporal pattern (Fig. 5.6). In general, the San San Pond Sak wetland tended to act as a CH₄ source, with fluxes typically ranging between 0 and 2 mg m⁻² h⁻¹. These are comparable to measurements for other tropical peatland systems; for example, Jauhiainen *et al.* (2005) reported mean CH₄ effluxes of 0.155 mg m⁻² h⁻¹ in Central Kalimantan, Indonesia. Some reported flux ranges were lower than those at San San Pond Sak; for example, Melling *et al.* (2005) found that CH₄ fluxes from a forested peatland in Sarawak, Malaysia were within the range -0.0061 – 0.0112 mg CH₄ m⁻² h⁻¹, a smaller range and magnitude than in the present study. Other tropical peatlands were found to produce CH₄ fluxes; for example, Inubushi *et al.* (2005), reported a mean CH₄ flux of 3.66 mg m⁻² h⁻¹ for a swamp forest in

Indonesia, greater than the majority of CH₄ fluxes recorded in San San Pond Sak. Overall, CH₄ fluxes were comparable with those reported for other tropical systems, although some recorded fluxes were much greater, as at the *R. taedigera* site in September 2007 when the mean flux was 12.6 mg CH₄ m⁻² h⁻¹. However, this unusually high mean value was driven by a single value of 69.9 mg CH₄ m⁻² h⁻¹. When compared to the median values, the mean values did not provide a fair representation of the CH₄ fluxes at the *R. taedigera* site (Fig. 5.1b). A similar effect was seen in February 2007 at the same site, when a relatively high mean flux of 7.0 mg CH₄ m⁻² h⁻¹ was driven by a single value of 32.5 mg CH₄ m⁻² h⁻¹. These individual unusually high CH₄ fluxes may be attributable to the mechanisms of CH₄ release from wetland systems. The release of methane as bubbles, known as ebullition, in wetland systems is well documented (Ueda *et al.*, 2000; Takakai *et al.*, 2005), and it is highly likely that the two unusually high individual CH₄ values resulted from the release of a bubble of CH₄ into the sampling chamber. As ebullition is a natural process, inclusion of these measurements within the dataset reflects the true nature of the extensive spatial and temporal variation of CH₄ within wetland systems.

As this dataset only takes account of fluxes from the surface of the peat, it is likely that total CH₄ efflux from the system exceeded, perhaps greatly, that measured due to its release *via* alternative pathways. For example, previous research has shown that substantial quantities of CH₄ may be released from peat after being transported upwards through vegetation (Nouchi *et al.*, 1990; Wason *et al.*, 1997; Nisbet *et al.*, 2009). It is highly probable that this pathway of CH₄ release was also present in the San San Pond Sak wetland system to some extent, explaining why CH₄ efflux from this near-permanently flooded system was low according to the data obtained, when it would be expected to be greater. Konnerup *et al.* (2010) present evidence for CH₄ flux from *Cyperus* species, but

there is no current data available for potential gas transport through the other vegetation species in this study.

5.4.2 Diurnal variation in fluxes

Significant diurnal variation in CO₂ fluxes was apparent at the sites dominated by *C. panamensis* and *Cyperus* sp., whereas the *R. taedigera* site showed no diurnal variation. These differing patterns were probably attributable to differences in the dominant vegetation type. The *C. panamensis* and *Cyperus* sp. sites showed a similar pattern in which CO₂ efflux peaked in mid-afternoon before decreasing overnight (Fig. 5.7). This trend may reflect the strong diurnal pattern of photosynthetic activity within the dominant vegetation and the time lag required for photoassimilates to be transported to the roots. Plants are known to exude both photoassimilates and O₂ into peat (Joabsson *et al.*, 1999; Singh, 2001; Crow and Wieder, 2005; Ding *et al.*, 2005). The release of O₂ creates localised oxic zones around roots, while the release of photoassimilates into the peat stimulates microbial respiration by providing new substrate material (Ding *et al.*, 2005).

The similar diurnal patterns for CO₂ efflux suggest that both *C. panamensis* and *Cyperus* sp. exhibited similar lag-times before significant quantities of recently produced photoassimilate were released to the peat. This similarity was unexpected as *C. panamensis* is a woody tree species whereas *Cyperus* sp. is a sedge species, which generally have shorter lag-times (Kuzyakov and Domenski, 2000; Kuzyakov and Cheng, 2001; Phillips *et al.*, 2008; Davidson and Holbrook, 2009; Mencuccini and Holtta, 2009; Savage *et al.*, 2009; Konnerup *et al.*, 2010). The transport velocity within the phloem is similar in trees and sedges but, as the latter are generally much shorter, there is a shorter physical distance for the photoassimilates to travel (Kuzyakov and Gavrichkova, 2010). However, it is possible that the time required for photoassimilates to reach the roots

of *C. panamensis* was 24 hours longer than in *Cyperus* sp, resulting in what appears to be a similar time lag. The third site was dominated by *R. taedigera*, a palm species which possesses aerenchyma. This anatomical feature might mean that aeration of the peat around the roots remained relatively uniform throughout the diurnal cycle, rather than being dependent on the photosynthetic activity of the plants. The existence of a continuous supply of O₂ may have been responsible for the absence of any significant diurnal variation in CO₂ efflux at the *R. taedigera* site. There was no correlation with the diurnal pattern of solar radiation (Fig. 5.8), perhaps due to the lag time effect, so that the effect of increased photosynthesis occurring with increased solar radiation is not reflected in the peat fluxes until photoassimilate has been released to the peat, a process which could occur a few hours or even days later (Kurzyakov and Gavrichkova, 2010). There was a significant effect of temperature on CO₂ flux, reflecting the decline in the rate of respiration as temperature decreases; this is likely to have occurred overnight when temperatures drop.

Fluxes were measured at the *Cyperus* sp. site in both February and August 2009. Whilst the diurnal patterns of CO₂ fluxes at this site were comparable in both months, the magnitude of the fluxes were significantly different, although those measured at 0730 h were comparable (Fig. 5.7c). This may indicate that respiration in the peat was similar in both months and the differences in the magnitude of the fluxes were linked to the photosynthetic activity of the surface vegetation, and that an environmental variable such as the quantity of photosynthetically active radiation (PAR) received by plants during the day of sampling affected the functioning of the vegetation.

No diurnal variation in CH₄ flux was found at any of the sites examined, although the three study sites possibly displayed differing emission patterns which might have proved significant with greater replication,

particularly at the *C. panamensis* site. Previous studies have shown that the dominant surface vegetation may affect the rate of CH₄ efflux by providing substrates for methanogenic bacteria (Joabsson *et al.*, 1999) and potentially a pathway for CH₄ produced within the peat profile to the atmosphere following transport from the roots to the shoots (Wason *et al.*, 1997). In these processes, the dominant vegetation has the potential to increase or decrease CH₄ production within the peat depending on which of the processes is dominant (Ding *et al.*, 2005). The CH₄ fluxes at the *Cyperus* sp. site in February 2009 also did not differ significantly over time (Fig. 5.10c).

5.4.3 Comparison of fluxes in July and August 2007 and 2009

Fluxes of CO₂ at the *C. panamensis* and *Cyperus* sp. sites were lower in July than in August in both 2007 and 2009 (Fig. 5.11). In August 2009, the CO₂ flux at the *C. panamensis* site (520 mg m⁻² h⁻¹) was greater than any other value recorded for any site during the sampling period, and more than double that found in August 2007. The CO₂ flux for the *Cyperus* sp. site in August 2009 (506 mg m⁻² h⁻¹) was the highest recorded for this site and over five times greater than in August 2007. The *R. taedigera* site showed a similar pattern in 2007, but in 2009 the rates were reversed. In 2007, rainfall was 2-3 times greater in July than in August, suggesting that the water table was higher in the former month. This inference is supported by the CO₂ flux data for 2007 in view of previous evidence that increased CO₂ fluxes are often associated with lower water tables (Updegraff *et al.*, 1995; Jauhianen *et al.*, 2005; Hirano *et al.*, 2009; Schedlbauer *et al.*, 2009). However, in 2009, when rainfall was greater in August than in July, only the *R. taedigera* site exhibited greater CO₂ fluxes in July.

Cumulative rainfall was highest in August 2009 (Table 5.1), the month when CO₂ fluxes at the *C. panamensis* and *Cyperus* sp. sites were

greatest (Fig. 5.11). Cumulative rainfall was also greater in July and August 2009 than in 2007. Although previous studies (Updegraff *et al.*, 1995; Jauhianen *et al.*, 2005; Hirano *et al.*, 2009; Schedlbauer *et al.*, 2009) suggest that CO₂ efflux should be suppressed under such conditions, the present results demonstrate the opposite, suggesting that other, as yet unidentified, factors exert strong influences over CO₂ flux in this system. It is possible that this was due to other environmental factors which varied from day to day, such as air temperature, cloud cover and solar radiation fluxes. Cloud cover could potentially impact upon soil respiration by restricting the quantity of photosynthetically active radiation received by the plant, thereby impacting on the quantity of photoassimilate produced and subsequently released to the peat following transport to the roots. Similarly, the extent and duration of stomatal opening has the potential to impact on photosynthetic rate and O₂ production and its subsequent release to the peat *via* the roots (Thomas *et al.*, 1996; Watson *et al.*, 1997). Other events such as storms may also have affected fluxes. Tropical storms are more common during the wet season and can be accompanied by strong winds, causing litter deposition. During the wet season, when water tables are typically above the peat surface, decomposition of this material is likely to be low due to anoxic conditions. However, when the water table falls and the peat becomes aerated, oxic conditions will occur, resulting in increased aerobic decomposition of the litter deposited during periods of anoxic conditions, thereby increasing the flux of CO₂ (Miyajima *et al.*, 1997; Wright and Reddy, 2001; Schwendenmann *et al.*, 2003; Jauhiainen *et al.*, 2005; Battle and Golladay, 2007; Guo *et al.*, 2008). The dominant vegetation species will also be linked to litter deposition during storms as litter quality influences substrate availability to the microbial community (Wight *et al.*, 2011).

On average, the San San Pond Sak wetland system was a source of CH₄ in July and August 2007 and 2009 (Fig. 5.13). CH₄ fluxes were greater at

all study sites in August 2009 than in any other month or year examined. It is likely that these high fluxes were linked to an increase in the height of the water table as rainfall was greatest in August 2009, creating anoxic conditions suitable for CH₄ production. Although scrutiny of the CH₄ data alone might suggest that oxidation of CH₄ to CO₂ would also have been suppressed by the anoxic conditions required to produce CH₄, CO₂ flux was also greatest in August 2009, indicating that oxic conditions must have existed within the peat to allow its production. These observations suggest the existence of both oxic and anoxic zones within the peat, even in the absence of an oxic surface layer, due to influences other than the water table, the most likely source being the roots of the dominant vegetation. There is evidence that up to 90% of the CH₄ produced within peat profiles is oxidised to CO₂ in the oxic surface layer (Bachoon *et al.*, 1992; Le Mer *et al.*, 2001). The results from the present study suggest the presence of an oxic layer at all sites in July and August 2007 and July 2009, but not in August 2009 at the *R. taedigera* and *C. panamensis* sites.

The CO₂ fluxes recorded in the present study are within the range reported for other tropical wetland systems (Table 2.1) during the dry season, but were generally lower during the wet season. This contrast may have occurred because the San San Pond Sak wetland is near-saturated throughout the annual cycle, whereas other tropical wetlands exhibit greater draw-down of the water table during the dry season and, as a result, may not reach, or take longer to reach, saturation during the wet season. CO₂ fluxes were generally at least one order of magnitude greater in the San San Pond Sak wetland than in northern peatlands (Thomas *et al.*, 1996; Crow and Wieder, 2005).

Tropical wetlands are generally sources of CH₄ and the fluxes measured in this study were comparable to those reported for other tropical wetlands (Chimner, 2004; Hadi *et al.*, 2005; Jauhiainen *et al.*, 2005), although

saturated tropical wetlands typically produce CH₄ fluxes exceeding those found in the present study, for example, a meta-analysis by Couwenberg *et al.* (2010) found average CH₄ fluxes in SE Asian peatlands of 3 mg m⁻² h⁻¹ which was greater than the majority of CH₄ fluxes found in this study. However, it is possible that total CH₄ production in the San San Pond Sak peatland exceeded the surface fluxes recorded if alternative pathways of CH₄ release to the atmosphere are present in this system.

In conclusion, CO₂ and CH₄ fluxes varied strongly on both short and long timescales. On an annual basis, the CO₂ flux pattern was similar for all three sites but varied in magnitude, with the *C. panamensis* site generally having the greatest CO₂ flux and the *Cyperus* sp. site the lowest. CH₄ fluxes showed no clear flux pattern, although there was an overall efflux at all three sites. Whilst CO₂ fluxes were correlated with monthly rainfall, no similar correlation was detected for CH₄ fluxes; thus, rainfall clearly influences gas fluxes from peatlands but is not the only controlling factor. An effect of dominant vegetation species was clearly apparent, as evidenced by the significant differences in CO₂ fluxes between sites (Fig. 5.1). The variation in fluxes over both long and short timescales has potentially important implications for predictions of the impact of climate change on CO₂ and CH₄ fluxes. The observed influence of the dominant vegetation demonstrates that peatlands dominated by different vegetation types may exhibit widely varying fluxes, with the result that rigorous and detailed sampling regimes are needed to accurately represent the temporal variation in fluxes within such systems.

CHAPTER 6. VARIATION IN GAS FLUXES FROM 0 - 2 M

DEPTH WITHIN THE PEAT PROFILE

6.1 Introduction

Carbon dioxide (CO₂) is produced within the profiles of tropical peatlands and released from their surface to the atmosphere. The two major sources of CO₂ are microbial activity and root respiration. As aerobic decomposition produces CO₂ in the better aerated portions of the profile, the greatest production of CO₂ is in the surface layers during periods when the water table falls (Furukawa *et al.*, 2005; Jauhiainen *et al.*, 2005; Couwenburg *et al.*, 2010). Fresh deposition of litter onto the peat surface can also increase CO₂ fluxes by providing labile carbon and nutrient inputs (Hirano *et al.*, 2009; Williams and Yavitt, 2010). Below the water table, CO₂ production from microbial decomposition is suppressed by the waterlogged conditions which favour anaerobic decomposition (Jackson *et al.*, 2009). Root respiration contributes to CO₂ production throughout the profile, and estimates of the percentage of CO₂ efflux from the surface peat layer which originate from root respiration vary from 26-90 % depending on geographical location and vegetation type (Raich and Schlesinger, 1992; Hanson *et al.*, 1993; Rouhier *et al.*, 1996; Andrews *et al.*, 1999). A study by Behera *et al.* (1990) indicated that 51% of the total CO₂ efflux from a tropical forest soil in India originated from root respiration, and estimates of 50% are commonly used for tropical wetlands (Townsend *et al.*, 1995; Chimner and Ewel, 2005). The species of vegetation present affects rooting depth and density within the peat profile and hence the depth to which root respiration, exudates and oxidation of peat using oxygen conducted down through the plant and released from roots influence CO₂ and CH₄ production (Watson *et al.*, 1997; Joabsson *et al.*, 1999; Frenzel *et al.*, 2000; Schwendenmann and Veldkamp, 2006; Konnerup *et al.*, 2010; Fritz *et al.*, 2011). The death and decomposition of roots contributes the input of new organic matter at depth (Hanson *et al.*, 2000; Personeni and Loiseau 2004; Crow and Wieder, 2005).

Tropical peatlands vary in the depth and extent of peat deposits. Previous research indicates that Amazonian wetlands may be up to 5.9 m in depth

(Lahteenoja *et al.*, 2009), while in Asia depths of up to 10 m are common (Page *et al.*, 1999) and in rarer cases up to 20 m (Shimada *et al.*, 2001). The depth of peat near the centre of San San Pond Sak is c. 8 m (Phillips *et al.*, 1997) but decreases to a depth of c. 2-3 m at some points towards the edge of the deposit due to its domed nature (*cf.* Section 3.1).

The recalcitrance of peat is believed to increase with depth due to: (i) a decrease in labile carbon as the fraction of litter that is easily degradable is decomposed in the surface horizons; (ii) anaerobic conditions resulting from the greater saturation of the peat with water cause the majority of decomposition processes to occur in the surface horizons due to cyclical wetting and drying and re-wetting as the water table fluctuates (Bragazza *et al.*, 2006; Hashimoto *et al.*, 2007); and (iii) decreased nutrient availability and hence reduced microbial activity (Putkinen *et al.*, 2009). In particular, vegetation inputs which are rich in carbon but poor in nitrogen and phosphorus are likely to decrease available nutrients at depth as available nutrients are consumed in surface processes (Qualls *et al.*, 2000; Williams and Yavitt, 2010). The changes in the chemistry of the peat constituents with increasing depth (i.e. decreases in bioavailable carbon and nutrients) and the gaseous environment (increasingly anaerobic) impact upon the potential microbial community (Bragazza *et al.*, 2006; Jackson *et al.*, 2009). The deeper peat is thought to be the primary source of CH₄ fluxes as anaerobic decomposition predominates under the prevailing anoxic conditions. This CH₄ diffuses upwards through the peat profile to the boundary between the anoxic/oxic layers, which occurs when the water table falls below the surface. Above this boundary and within the oxic layer, up to 90% of the CH₄ is oxidised to CO₂ by methanotrophy (Bachoon *et al.*, 1992; Le Mer *et al.*, 2001; Hirano *et al.*, 2009), although there is also the potential for CH₄ emissions from vascular plants and from ebullition, which are not included in estimates of fluxes from peat surfaces (Whiting and Chanton, 1993; Watson *et al.*, 1997; Ding *et al.*, 2005). Reported experimental results have varied; thus, although most provide evidence of CH₄ transport through some plant species, others obtained under different conditions have shown no transport effect of plants on CH₄ efflux; instead, the transport of oxygen by plants into the soil has an inhibitory effect on CH₄ production within the rooting zone (Grunfeld and Brix, 1999; Kutzbach *et al.*, 2004; Dinsmore *et al.*, 2009).

However, some research suggests that the contribution of deep peat to gas fluxes is more important than previously thought. For example, Scanlon *et al.* (2000) highlighted the differing characteristics of peat from the surface and deeper layers. They found that the peat at depth was more compressed and cohesive than the loosely structured surface horizons and suggested that, when considered on a volumetric rather than a gravimetric basis, there is a fair degree of consistency of CO₂ production throughout the profile. However, under natural conditions, the contribution of CO₂ produced at depth to surface fluxes would be affected by other factors such as diffusion and solubility, with the potential to trap and concentrate CO₂ at depth (Schwendenmann *et al.*, 2006). Other studies suggest that, although peat at various depths contributes to CO₂ production, the surface horizons are responsible for the majority of the efflux. For example, Schwendenmann *et al.* (2006) found that over 75% of the CO₂ produced in a tropical wet forest in Costa Rica could be attributed to the upper 0.5 m of the peat profile.

As discussed previously, the contribution of peat and root respiration to CO₂ and CH₄ fluxes in peatlands varies with depth and surface vegetation. It is important to understand the contributions of fluxes from depth in order to assess the potential for CO₂ and CH₄ production under varying environmental conditions for use in modelling fluxes under future climatic scenarios.

The aim of this investigation was to assess the contribution of peat from 0 - 2 m depth in the profile to the surface CO₂ and CH₄ fluxes and quantify peat characteristics through the profile. It was hypothesised that the peat will become increasingly nutrient-poor with increasing depth, and that CO₂ production will decrease whilst CH₄ production increases with depth.

6.2 Materials and methods

Two experiments were carried out to investigate peat characteristics and gas fluxes throughout the profile at the San San Pond Sak wetland.

- 1) *ex situ* incubation of peat from different depths in the profile

2) *in situ* monitoring of CO₂ and CH₄ fluxes from the surface and three depths in the profile

Peat cores were collected for detailed laboratory analysis. The three sites examined were located at either end of the transect and approximately in the centre. The three sites were identified by their dominant vegetation species *i.e.* *Raphia taedigera* (palm swamp), *Camposperma panamensis* (forest swamp) and *Cyperus* sp. (bog plain) (*cf.* Section 3.1 for further details).

Cores were taken using a simplified lightweight piston corer (Fisher, 1992) designed to remove intact undisturbed cores using a vacuum (Fig. 6.1).

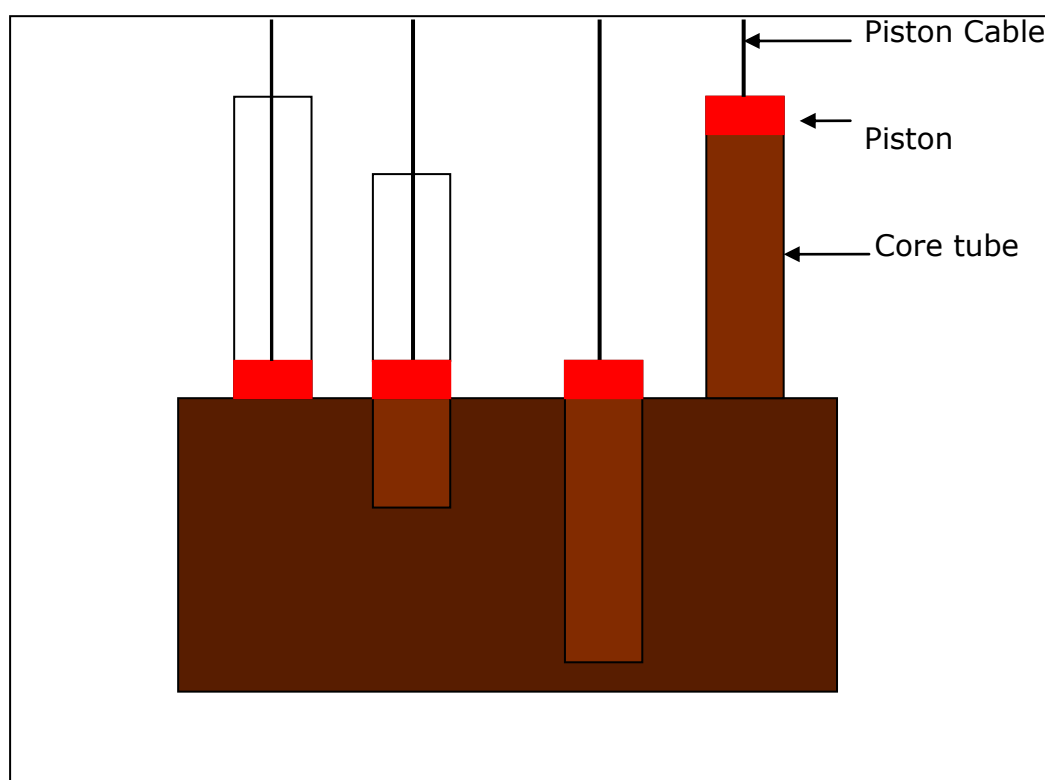


Figure 6.1. Peat sampling procedure. The piston cable was secured above the area to be cored and the piston placed on the peat surface to create a seal. The core tube was then pushed into the peat and when the required depth was reached the piston was locked in place and the assemblage removed. The vacuum created by the piston seal minimised compaction and ensured the peat sample remained in the core tube when removed from the peat.

At each site, four 1 m deep cores were taken, one of which was extended to a depth of 2 m. Cores were taken within 10 m of the path, giving preference to locations which were relatively free of major vegetation due to the impossibility of coring through the largest roots found close to mature trees. Each core

location was at least 20 m from adjacent coring locations. The coring tubes were 7.6 cm in internal diameter.

To minimise disturbance after removing the cores from the peat profile, pre-cut foam disks were inserted into the top of the tube to a distance of 1 cm above the surface of the core and plastic caps were secured over both ends of each tube. The cores were kept upright during transport to the laboratory on Isla Colon, where they were stored upright overnight at 4 °C. On the following day, the cores were removed from the refrigeration unit and placed outside in the shade to warm to the ambient temperature (c. 26-28 °C). Once they had warmed, any settled surface water was siphoned off in separate 10 cm intervals. After removing all surface water, the remaining peat material was carefully cut into 10 cm segments. Once the core tubing had been cut through, a thin, stiff plastic sheet was inserted between adjacent segments before quickly inverting the segment and capping both ends of the tube. Water loss was minimised during this process. Segments were transferred to the laboratory to settle and equilibrate overnight at 24 °C. Following equilibration, the depth of pooled surface water was generally greater than at the time of sampling due to disturbance of the loose surface layer. To account for this, the 0-30 cm horizon was counted as one mixed segment and separate 10 cm deep surface cores were collected in the field, using 10 cm lengths of the corer tubing.

6.2.1 Peat core analysis

Each core segment was weighed and its redox determined using a KDCMPtB11 redox probe (Thermo Electron Corporation, UK) and CO₂ and CH₄ fluxes were measured by headspace sampling which provided gas samples for CO₂ and CH₄ analysis. To obtain these samples, a 10 cm head space fitted with a rubber Suba-Seal® was attached sequentially to each core segment. Each headspace was flushed with hydrogen gas for 20 s before sampling 25 ml of headspace air using a syringe through the Suba-Seal®. Headspace samples were taken 0 and 10 minutes after fitting the headspace. Samples were injected into prepared 12 ml evacuated gas vials and transported to Nottingham for analysis of CO₂ and CH₄ concentrations using a Shimadzu Gas Chromatograph (Model GC-2014,

Shimadzu Corporation, Japan) using a flame ionising detector for CH₄ detection and a thermal conductivity detector for CO₂ detection.

Twenty ml samples of pore water were collected using Rhizon[®] samplers with a pore diameter of 0.45 µm within their ceramic walls. Rhizon[®] samplers consist of 20 cm long ceramic tubes which, when placed in soil, extract soil pore water samples when tension is applied by attaching a syringe to the end of the tube and pulling out and securing the plunger. The pore size of the Rhizon[®] sampler walls is sufficiently small to prevent penetration of soil particulate matter during sampling. The samplers were inserted diagonally through each core segment after being soaked in 0.2 M HCl for 5 min before being rinsed with deionised water to remove any fine soil material from the pore spaces within their walls.

The root biomass was removed from each peat segment and living roots were identified from their colour and condition; these were washed in deionised water and air-dried. Root biomass was then calculated in g per g of peat material. Soil dry weight was measured for sub-samples taken from each core segment to determine bulk density. These sub-samples were oven-dried at 70 °C for 24 h. The remaining peat was air-dried, except for the 20-30, 50-60 and 80-90 cm segments, for which half was air-dried and half was kept fresh.

6.2.2 Analysis of dried peat

The air-dried peat was analysed for pH, and for total carbon, nitrogen and phosphorus content using the procedures described in Section 3.2.2.

6.2.3 Porewater sample analysis

Porewater samples were analysed to determine total phosphorus, nitrogen and dissolved organic carbon content as described in Section 3.2.2.2.2.

6.2.4 In situ flux measurements

In situ gas fluxes were sampled at depths of 30, 60 and 100 cm below the surface, and for surface samples collected concurrently.

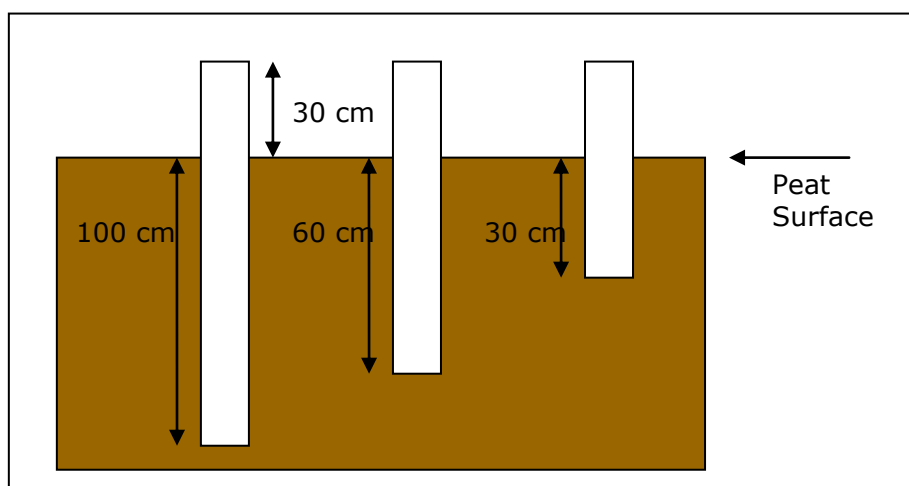


Figure 6.2. Positioning of diffusion tubes within the peat profile.

Diffusion tubes 5.08 cm in diameter were placed in the peat using a 3.81 cm diameter borer inserted to the correct depth before placing the sample tube over the borer and removing the borer (Fig. 6.2). Diffusion tubes were covered with ventilated caps to prevent infiltration of rainwater but allow the efflux of gases. The tubes were left to equilibrate for several months before taking gas samples by attaching a 5 cm headspace containing a motorised fan assembly positioned to be within 3 cm of the water table within the diffusion tube. When collecting samples, the headspaces were sealed to the tube and the fan was turned on. Samples were collected using a 25 ml syringe after 0, 2, 10 and 20 minutes using a Suba-Seal[®] fitted to the headspace and injected into prepared 12 ml vacuumed gas vials. Samples were shipped to Nottingham for analysis using a Shimadzu Gas Chromatograph (Model GC-2014, Shimadzu Corporation Japan) using a flame ionising detector for CH₄ detection and a thermal conductivity detector for CO₂ detection. CO₂ and CH₄ fluxes were expressed on a mg m⁻² h⁻¹ basis. Surface samples were also collected using a 10 cm headspace placed directly on the peat surface using the sampling protocol described in Section 3.2.1. Water table depth and peat temperature were recorded at the time of sampling.

6.2.5 Data Analysis

All statistical analyses were performed using Genstat version 11 (Lawes Agricultural Trust, Rothamsted Experimental Station). All CO₂ and CH₄ fluxes were tested for normality before using a Shapiro-Wilk's test to test for significance ($p < 0.05$) and visual inspection of quantile–quantile plots. If the null hypotheses were rejected, the data were transformed to meet the assumptions of normality. Peat characteristics were analysed using separate analyses of variance (ANOVA), with depth and site as fixed effects. *In situ* fluxes were analysed using separate ANOVAs for July and August to test for depth and site effects. ANOVA was performed to test for effects of sampling month, site, depth and interactions on fluxes. *Ex situ* fluxes were analysed in two groups; the first comprised the 15–95 cm depth samples, with site, depth and interactions as fixed effects and the second comprising the cores that extended to 2 m depth to test for site and depth effects. The effects of peat characteristics on fluxes were analysed using linear or quadratic regression analysis after visual inspection of the spread of data to determine which was more appropriate

6.3 RESULTS

6.3.1 Peat characteristics

6.3.1.1 Peat profile characteristics and changes with depth

Gravimetric moisture content was extremely high throughout the profile, ranging from 89 to 99 % (Table 6.1). pH ranged from 3.5 to 4.5 (Table 6.2) and was highest in the surface peat layer, decreased sharply at 40 cm depth, and then remained relatively constant through the profile apart from at the *C. panamensis* site, where pH increased slowly from a minimum at the surface to a depth of 1 m. The peat was generally weakly reduced throughout the profile (Table 6.2), with mean redox potentials for the entire profile of 282, 335 and 356 mV at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites, respectively.

Loss on ignition (LOI) was generally extremely high, ranging between 82 and 99 %, except for distinct layers of higher ash content at depths of 110–140 cm and

150 cm at the *R. taedigera* and *C. panamensis* sites, respectively (Fig. 6.3b). Dry bulk density (BD) was very low and always $<0.09 \text{ g cm}^{-3}$ (Fig. 2e). The BD of the surface peat (0-10 cm) was lowest at the *Cyperus* sp. site (c. 0.02 g cm^{-3}), but the values for depths between 10-120 cm were generally similar, ranging from 0.03 to 0.05 g cm^{-3} at all sites, although a marked increase was apparent at 120 and 140 cm for the *R. taedigera* and *C. panamensis* sites, respectively. The peak in BD at the *R. taedigera* site corresponded to a much lower LOI and high pH at the same depth.

Root dry biomass did not vary significantly with depth within the upper 100 cm and was close to zero at depths $>110 \text{ cm}$ (Fig. 6.4). The values were greatest at the *Cyperus* sp. site for depths between 0-65 cm, with maximum values of c. 360 g m^{-2} . However, at greater depths (75-105 cm), root biomass was greatest at the *R. taedigera* site, although the values were distinctly lower (150 g m^{-2}) than in the surface layers at the *Cyperus* sp. site. Root biomass was consistently lowest for *C. panamensis* throughout the profile.

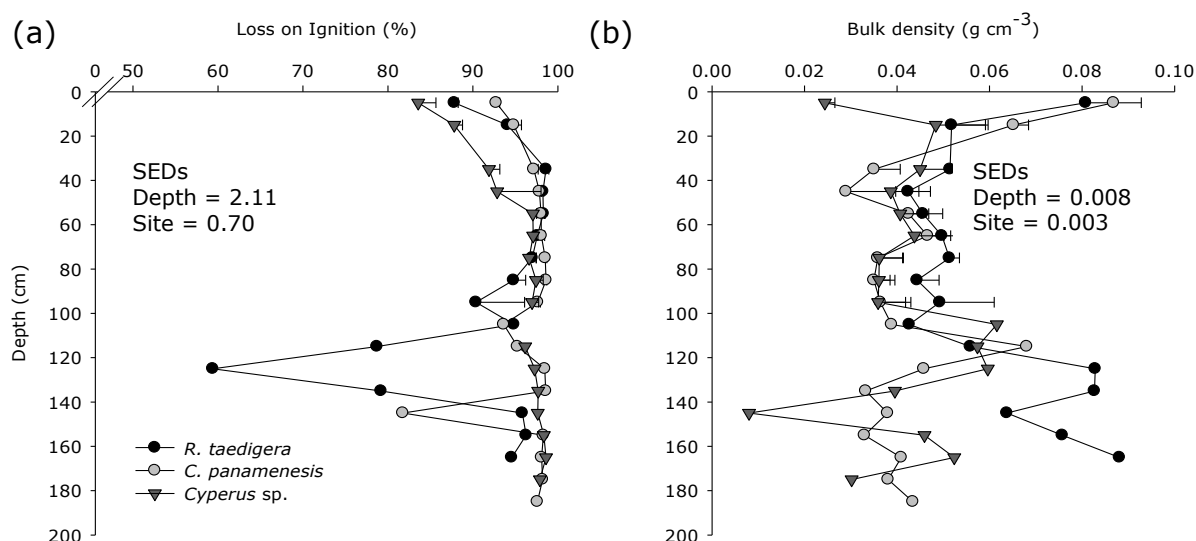


Figure 6.3. (a) Mean loss on ignition and (b) bulk density for each site; $n=5$ for 0-10 cm and $n=4$ for 10-100 cm. Single standard errors of the mean are shown for depths $\leq 100 \text{ cm}$. Unreplicated measurements were made for depths $>100 \text{ cm}$. ANOVA outputs 5-95 cm ($n=4$) are:

a) Depth: $F_{8,108} = 7.32$, $p < 0.001$
 Site: $F_{2,108} = 4.18$, $p < 0.05$
 Site \times Depth: $F_{16,108} = 8.31$, $p < 0.001$
 ANOVA outputs single cores ($n=1$) 15-185 cm depth:
 a) Depth: $F_{17,61} = 1.54$, $p = 0.1$
 b) Depth: $F_{17,62} = 1.19$, $p = 0.3$

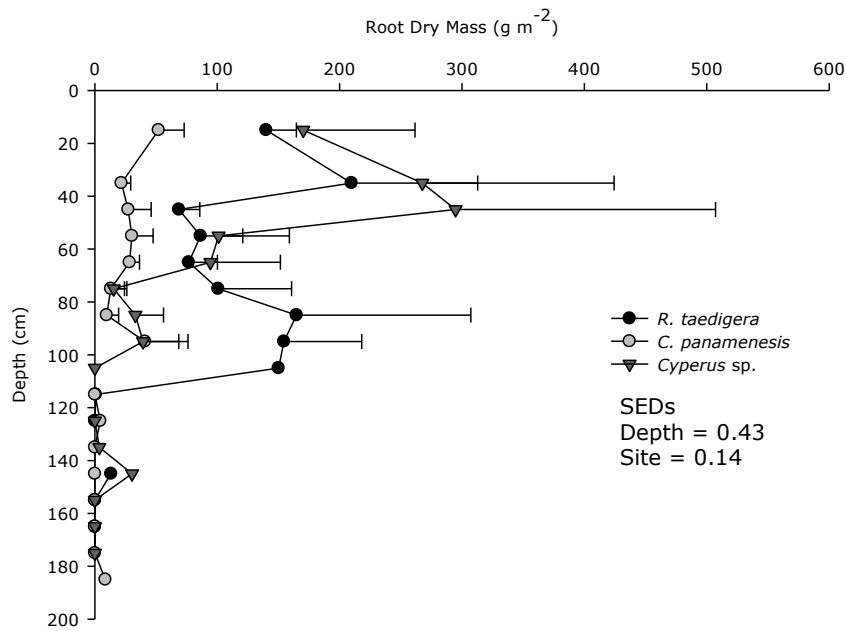


Figure 6.4. Mean dry root biomass for each site; $n=5$ for 0-10 cm and $n=4$ for 10-100 cm. Single standard errors of the mean are shown for depths ≤ 100 cm. Unreplicated measurements were made for depths >100 cm. ANOVA outputs 5-95 cm ($n=4$ at each site) are: Depth: $F_{7,95}=1.60$, $p=0.15$; Site: $F_{2,95}=2.79$, $p=0.11$; Depth \times Site: $F_{14,95}=1.44$, $p=0.16$. ANOVA Single cores ($n=1$ at each site) 15-185 cm: Depth: $F_{16,47}=1.96$, $p=0.056$.

Organic carbon (OC) content differed significantly with site and depth (Fig. 6.5a). The values for 0-90 cm depths were greatest at the *R. taedigera* site, followed successively by the *C. panamensis* and *Cyperus sp.* sites. At depths >90 cm, OC content did not vary with depth at the *Cyperus sp.* site. *C. panamensis* had a much lower OC content at 100 cm depth, below which the values increased. *R. taedigera* had the greatest OC content at all depths except between 110-140 cm where the lowest OC content of 330 mg g^{-1} peat occurred. This corresponded to a peak in pH and BD and a much lower LOI for the same depth and site.

Total nitrogen (TN) content varied significantly with site, depth and the site \times depth interaction was also significant (Fig. 6.5b). TN content in the 0-70 cm layers peat was greatest at the *R. taedigera* site below which the values decreased. TN content of peat at the *C. panamensis* and *Cyperus sp.* sites were similar at depths <50 cm but the values were lower at the *Cyperus sp.* site at greater depths. At depths >120 cm peat from the *R. taedigera* site had the lowest TN content.

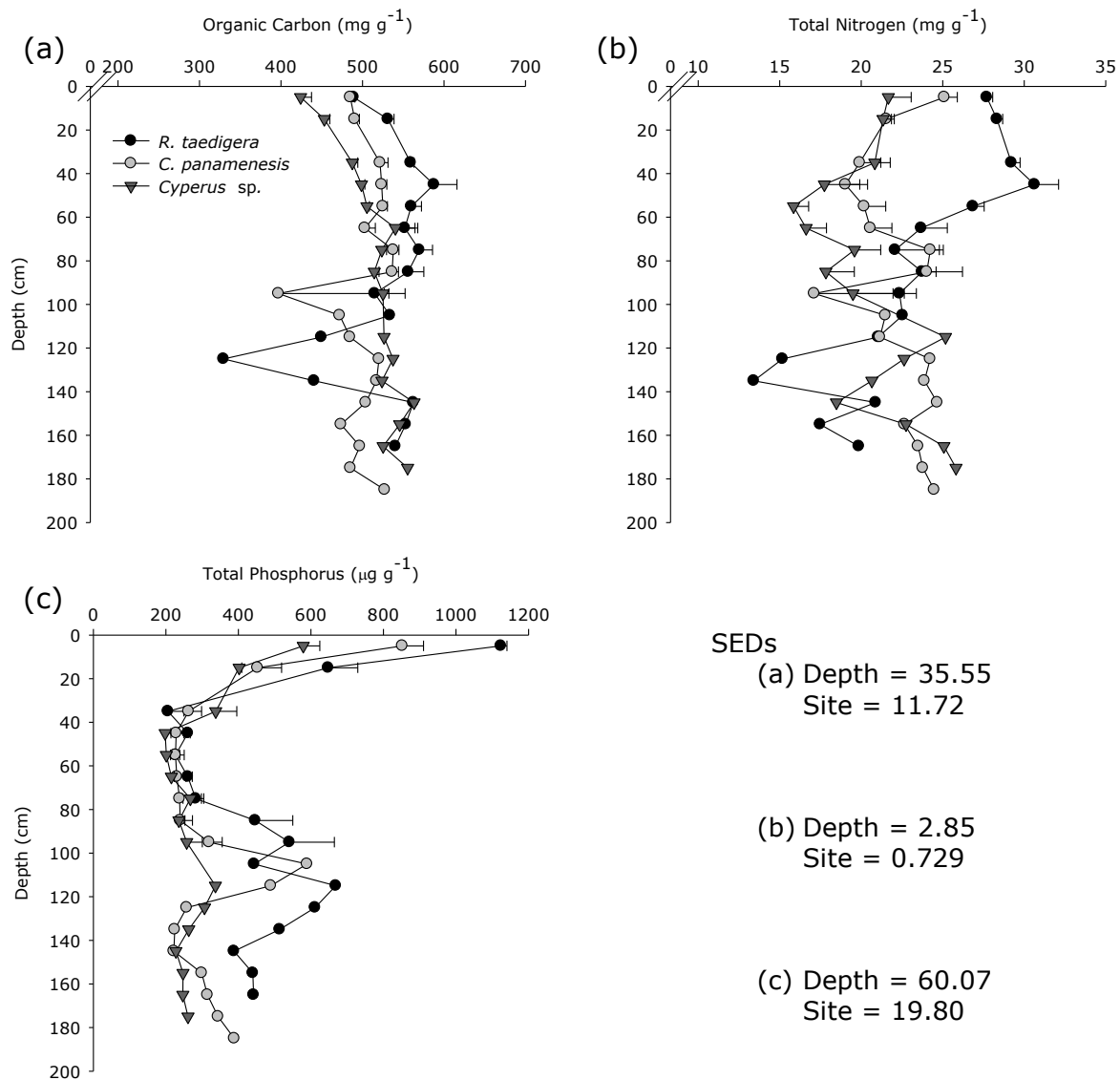


Figure 6.5. Content of a) organic carbon, (b) total nitrogen and (c) total phosphorus; $n=5$ for 0-10 cm and $n=4$ for 10-100 cm. Unreplicated measurements were made for depths >100 cm. Single standard errors of the mean are shown for depths ≤ 100 cm. ANOVA summaries 5-95 cm ($n=4$ at each site) were:

- a) Depth: $F_{8,109} = 3.38, p < 0.05$
 Site: $F_{2,109} = 8.65, p < 0.001$
 DepthxSite: $F_{16,109} = 1.14, p = 0.3$
 b) Depth: $F_{8,109} = 2.96, p < 0.05$
 Site: $F_{2,109} = 39.00, p < 0.001$
 DepthxSite: $F_{16,109} = 5.21, p < 0.001$
 c) Depth: $F_{8,109} = 65.45, p < 0.001$
 Site: $F_{2,109} = 26.11, p < 0.001$
 DepthxSite: $F_{16,109} = 5.21, p < 0.001$

ANOVA Single cores ($n=1$ at each site) 15-185 cm:

- a) Depth: $F_{16,46} = 0.88, p = 0.6$
 b) Depth: $F_{16,46} = 0.64, p = 0.8$
 c) Depth: $F_{16,46} = 3.00, p < 0.05$

Table 6.1. Characteristics through the peat profile. 1 = *Raphia taedigera* site, 2 = *Campnosperma panamensis* site and 3 = *Cyperus* sp. Site. \pm SE shown with $n = 5$ replicates for depth level 0-10 cm, $n = 4$ replicates only for depth levels <100 cm. Depths >100 cm represented by a single core at each site.

ANOVA summaries of variance with depth for: Gravimetric Water Content $F_{1,147}=10.02$, $p=0.002$
 Bulk Density $F_{1,147}= 5.81$, $p=0.17$
 Root Biomass $F_{1,132}=19.05$, $p<0.001$

Depth (cm)	Gravimetric Water Content (%)			Bulk Density (g cm ⁻³)			Root Biomass (g m ⁻²)		
	1	2	3	1	2	3	1	2	3
5	90.2 \pm 0.9	89.4 \pm 0.7	97 \pm 0.2	0.081 \pm 0.006	0.087 \pm 0.006	0.024 \pm 0.002	* *	* *	* *
15	94.1 \pm 0.8	92.8 \pm 0.5	96 \pm 0.3	0.044 \pm 0.017	0.061 \pm 0.003	0.058 \pm 0.009	140.1 \pm 24.6	52.1 \pm 20.8	283.9 \pm 67.6
35	94.2 \pm 0.9	95.8 \pm 0.7	95 \pm 0.5	0.041 \pm 0.013	0.035 \pm 0.006	0.045 \pm 0.011	209.8 \pm 103.1	21.8 \pm 7.6	334.4 \pm 159.0
45	95.0 \pm 0.5	96.7 \pm 1.2	94 \pm 1.2	0.034 \pm 0.010	0.029 \pm 0.011	0.039 \pm 0.009	68.7 \pm 17.1	27.3 \pm 18.7	368.5 \pm 225.9
55	94.7 \pm 0.5	94.8 \pm 0.5	90 \pm 0.6	0.036 \pm 0.011	0.042 \pm 0.004	0.041 \pm 0.005	86.3 \pm 34.5	30.3 \pm 17.3	126.5 \pm 58.0
65	94.4 \pm 0.3	94.8 \pm 0.7	94 \pm 0.8	0.040 \pm 0.011	0.047 \pm 0.007	0.044 \pm 0.006	76.7 \pm 23.4	28.3 \pm 8.2	118.1 \pm 58.5
75	94.1 \pm 0.3	95.7 \pm 0.5	96 \pm 1.1	0.041 \pm 0.012	0.036 \pm 0.005	0.036 \pm 0.005	100.8 \pm 60.0	13.1 \pm 13.1	19.2 \pm 8.9
85	94.5 \pm 0.2	95.7 \pm 0.2	95 \pm 0.8	0.035 \pm 0.011	0.035 \pm 0.003	0.036 \pm 0.003	164.8 \pm 142.4	9.7 \pm 9.7	41.3 \pm 24.5
95	93.9 \pm 0.9	95.8 \pm 0.7	96 \pm 0.7	0.039 \pm 0.015	0.036 \pm 0.007	0.036 \pm 0.006	154.6 \pm 63.5	41.0 \pm 35.1	49.4 \pm 31.0
105	94.5	94.9	*	0.043	0.039	0.062	150.1	*	0.0
115	93.9	92.7	97	0.056	0.068	0.057	0.8	0.0	*
125	90.4	94.9	96	0.083	0.046	0.060	0.0	4.4	0.0
135	90.5	96.1	96	0.083	0.033	0.040	*	0.0	3.7
145	92.2	95.6	94	0.064	0.038	0.008	13.2	0.0	30.5
155	91.4	96.3	95	0.076	0.033	0.046	0.0	0.0	0.0
165	89.8	95.5	95	0.088	0.041	0.052	0.0	0.0	0.0
175	58.8	95.6	95	0.262	0.038	0.030	*	0.0	0.0
185	33.8 [#]	94.7	*	1.077	0.043	*	*	8.6	* *

[#] The gravimetric water content is lower at this depth as this was a mineral soil found below the extent of the peat.

Table 6.2. Characteristics through the peat profile. 1 = *Raphia taedigera* site, 2 = *Campnosperma panamensis* site and 3 = *Cyperus* sp. Site. \pm SE shown with $n = 5$ replicates for depth level 0-10 cm, $n = 4$ replicates only for depth levels <100 cm. Depths >100 cm represented by a single core at each site.

ANOVA summaries of variance with depth for: pH $F_{1,107}=48.35$, $p<0.001$

Redox $F_{1,146}= 0.78$, $p=0.378$

Depth (cm)	pH			Redox (mV)		
	1	2	3	1	2	3
5	3.22 \pm 0.05	3.10 \pm 0.03	3.15 \pm 0.03	26 \pm 32	13 \pm 29	-15 \pm 23
15	3.29 \pm 0.03	3.09 \pm 0.05	* *	196 \pm 14	184 \pm 19	229 \pm 9
35	3.36 \pm 0.02	3.14 \pm 0.06	3.24 \pm 0.08	91 \pm 31	192 \pm 23	130 \pm 28
45	3.40 \pm 0.01	3.07 \pm 0.16	3.22 \pm 0.01	92 \pm 28	220 \pm 31	127 \pm 26
55	3.40 \pm 0.01	3.17 \pm 0.07	3.25 \pm 0.05	79 \pm 23	186 \pm 25	101 \pm 28
65	3.38 \pm 0.02	3.20 \pm 0.08	3.35 \pm 0.07	73 \pm 17	134 \pm 21	74 \pm 7
75	3.37 \pm 0.03	3.27 \pm 0.13	3.27 \pm 0.09	66 \pm 12	117 \pm 20	90 \pm 19
85	3.40 \pm 0.06	3.33 \pm 0.01	3.31 \pm 0.04	85 \pm 20	114 \pm 23	177 \pm 45
95	3.39 \pm 0.07	3.29 \pm 0.07	3.25 *	84 \pm 42	140 \pm 33	153 \pm 53
105	3.40		*	87	360	186
115	3.47	3.23	*	34	236	152
125	3.59		3.54	43	52	262
135	*		*	49	56	251
145	*	3.40	3.25	*	83	160
155	3.52		*	20	28	137
165	3.59	3.19	3.38	89	56	181
175	4.05	3.20	3.32	83	51	128
185	4.02	3.27	3.15	-27	44	*

Total phosphorus (TP) content also varied with depth (Fig. 6.5c; $p < 0.001$) and was greatest in the 0-10 cm layer at all sites. TP values were highest at the *R. taedigera* site ($1124 \mu\text{g P g}^{-1}$), followed successively by the *C. panamensis* ($852 \mu\text{g P g}^{-1}$) and *Cyperus* sp. sites ($579 \mu\text{g P g}^{-1}$). TP content decreased between 10-40 cm at all sites, remained relatively constant between 40-80 cm and then increased to a secondary peak between 110-120 cm at the *R. taedigera* and *Cyperus* sp. sites and 100-110 cm at the *C. panamensis* site. Of these secondary peaks, *R. taedigera* showed the highest value of $669 \mu\text{g P g}^{-1}$ and *Cyperus* sp. the lowest of $337 \mu\text{g P g}^{-1}$. TP content then decreased at greater depths at all sites. The profiles for TP content differed between sites ($p < 0.001$) as the values were generally greatest for *R. taedigera* followed successively by the *C. panamensis* and *Cyperus* sp. sites.

The carbon:nitrogen (C:N) ratio varied with depth (Fig. 6.6a, $p < 0.001$). The ratio for the 0-10 cm layer at the *R. taedigera* site of 17.7 was the lowest recorded value for all depths and sites. C:N ratios for *R. taedigera* peat generally increased with depth to a maximum of 31.6 at 150-160 cm. Ratios for *C. panamensis* peat also increased with depth to a maximum of 27.7 at 40-50 cm before decreasing again. The profile for the *Cyperus* sp. site was similar to those for *R. taedigera* and *C. panamensis*, increasing with depth to 70 cm before decreasing again. The profiles varied between sites as the C:N ratios were generally highest at the *Cyperus* sp. site followed successively by the *C. panamensis* and *R. taedigera* sites.

The carbon:phosphorus (C:P) ratio also varied with depth (Fig. 6.6b: $p < 0.001$). The values for all sites were lower in the 0-10 cm layer, but increased with depth to a peak of 3465 at 30-40 cm at the *R. taedigera* site and peaks of 2348 and 2570 respectively at 40-50 cm for the *C. panamensis* and *Cyperus* sp. sites. C:P ratio then decreased with depth all sites. There was no significant variation between sites for the C:P ratio.

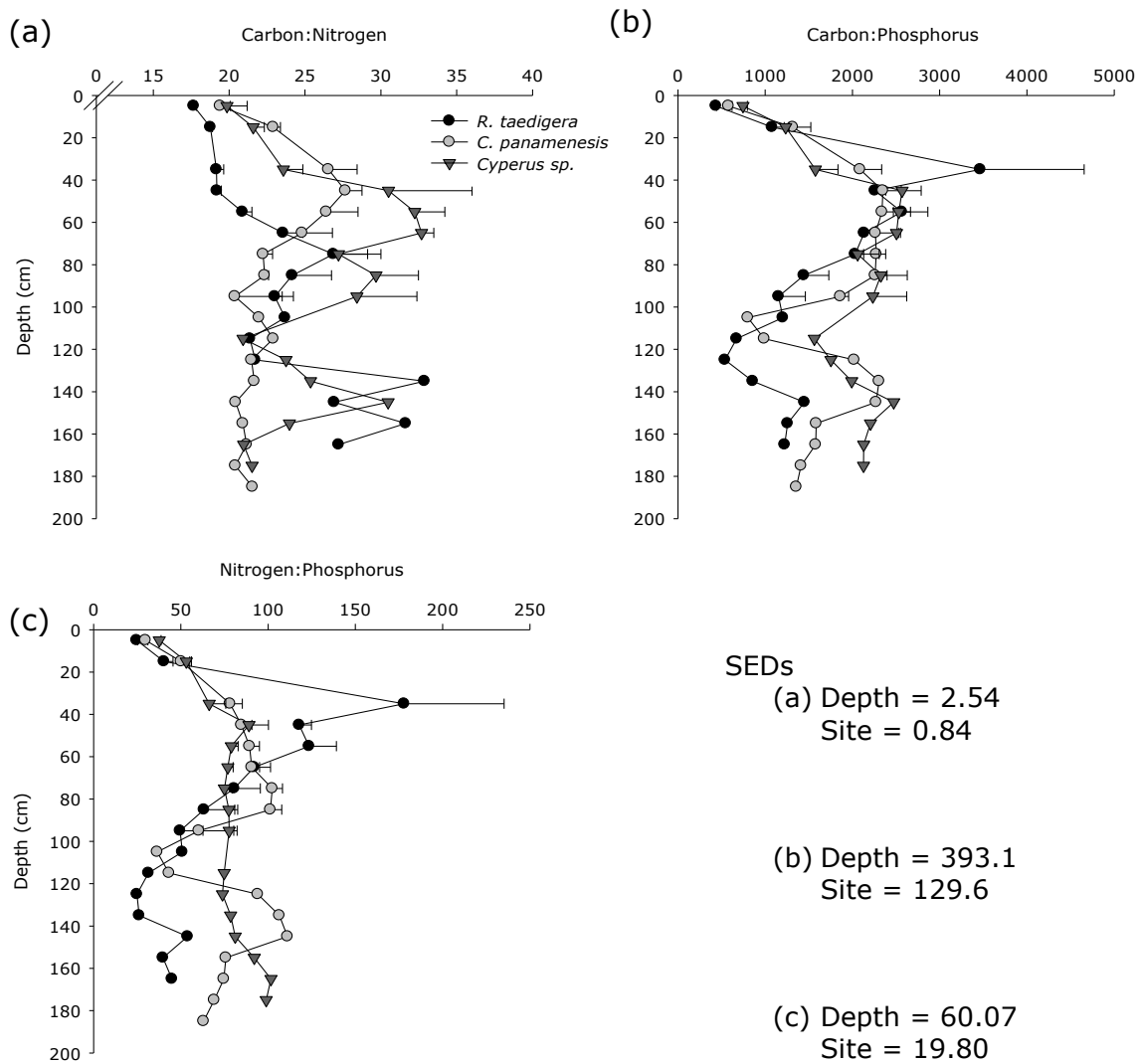


Figure 6.6. Ratios of a) Carbon:Nitrogen, (b) Carbon:Phosphorus, (c) Nitrogen:Phosphorus for each site; $n=5$ for 0-10 cm and $n=4$ for 10-100 cm. Unreplicated measurements were made for depths >100 cm. Single standard errors of the mean are shown for depths ≤ 100 cm. ANOVA summaries for depths of 5-95 cm ($n=4$ at each site) are:

- a) Depth: $F_{8,109} = 5.90, p < 0.001$
Site: $F_{2,109} = 19.24, p < 0.001$
DepthxSite: $F_{16,109} = 2.26, p < 0.05$
b) Depth: $F_{8,109} = 14.50, p < 0.001$
Site: $F_{2,109} = 0.51, p = 0.6$
DepthxSite: $F_{16,109} = 2.08, p < 0.05$
c) Depth: $F_{8,109} = 10.97, p < 0.001$
Site: $F_{2,109} = 26.11, p = 0.08$
DepthxSite: $F_{16,109} = 3.28, p < 0.001$

ANOVA Single cores ($n=1$ at each site) 15-185 cm:

- a) Depth: $F_{16,46} = 0.79, p = 0.7$
b) Depth: $F_{16,46} = 1.60, p = 0.1$
c) Depth: $F_{16,46} = 1.20, p = 0.3$

The nitrogen:phosphorus (N:P) ratio also varied with depth (Fig. 6.6c: $p < 0.001$) and showed profiles similar to those for the C:P ratio, as the values were greatest near the surface and decreased with depth. There was no significant variation between sites in the profiles ($p > 0.05$).

There was no significant effect of depth on the quantity of dissolved organic carbon (DOC) in the porewater, although the values varied greatly between sites (Fig. 6.7a). DOC was greatest at the *R. taedigera* site and lowest at the *Cyperus* sp. site throughout the profile, with the exception of 100-110 cm where the value was greatest at the *C. panamensis* site. Dissolved nitrogen (DN) content in the porewater did not vary significantly with depth but differed between sites (Fig. 6.7b), as is evident from the marked difference between the profiles for the *R. taedigera* site compared to the *C. panamensis* and *Cyperus* sp. sites. Values were invariably greatest for the *R. taedigera* site, peaking at 0.923 mg l^{-1} in the 0-10 cm layer and decreasing through the profile to a minimum of 0.420 mg l^{-1} . Profiles for the *C. panamensis* and *Cyperus* sp. sites were similar, with values ranging between $0.2\text{-}0.5 \text{ mg l}^{-1}$ and showing no clear trend with depth.

There was again no significant effect of depth on dissolved phosphorus (DP) content although the values differed between sites (Fig. 6.7c; $p < 0.001$). DP concentration was greatest at the surface of the *R. taedigera* site (0.37 mg l^{-1}) but decreased to c. 0.02 mg l^{-1} at depths $> 100 \text{ cm}$. The *C. panamensis* and *Cyperus* sp. sites had the lowest DP concentrations in the 0-10 cm layer of 0.07 and 0.03 mg l^{-1} .

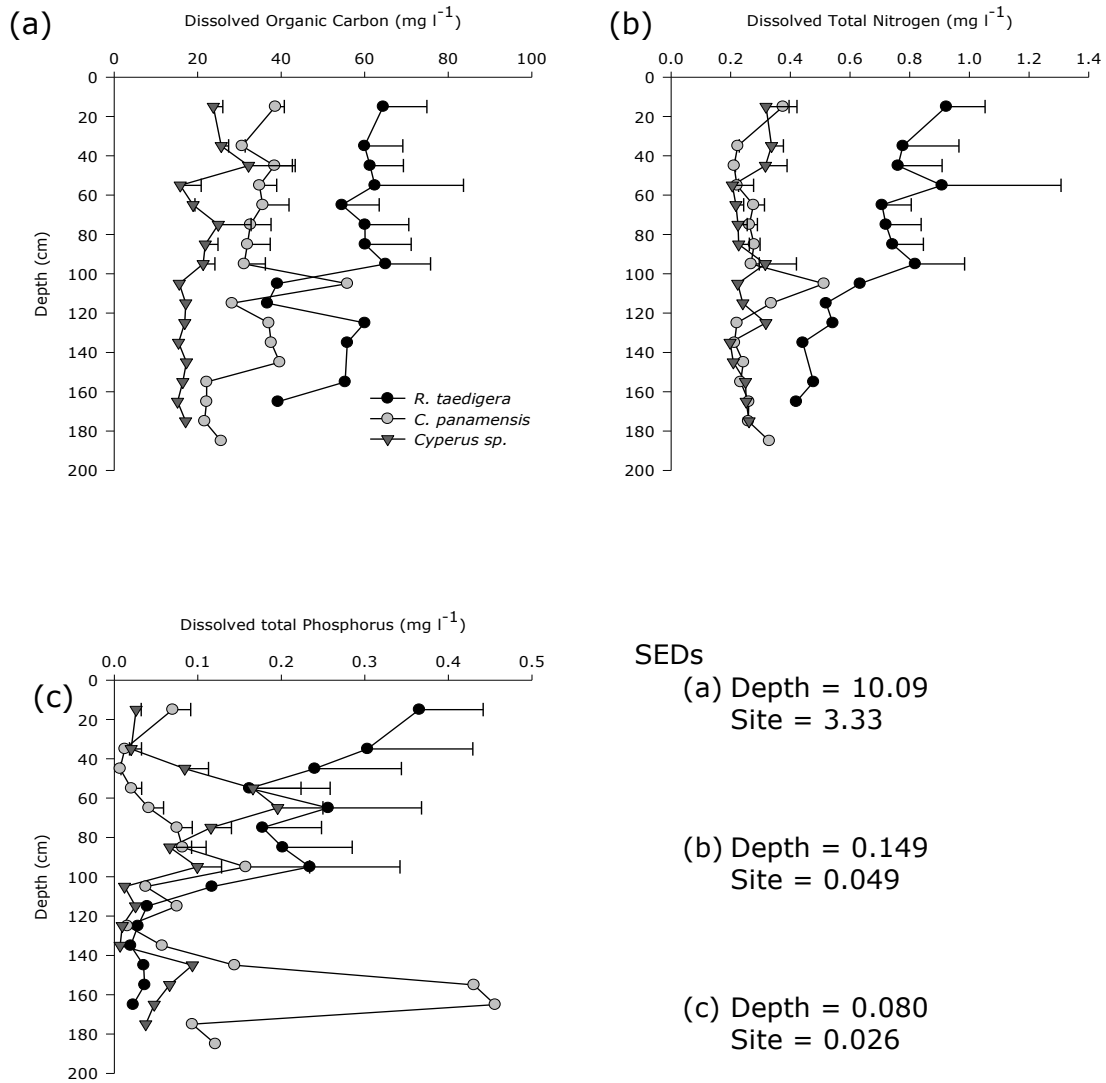


Figure 6.7. a) Dissolved organic carbon, (b) Dissolved total nitrogen, (c) dissolved total phosphorus in porewater from each site; $n=5$ for 0-10 cm and $n=4$ for 10-100 cm. Unreplicated measurements were made for depths >100 cm. Single standard errors of the mean are shown for depths ≤ 100 cm.

ANOVA outputs for depths of 5-95 cm ($n=4$ at each site) were:

- a) Depth: $F_{7,95} = 0.30$, $p=0.9$
 Site: $F_{2,95} = 56.20$, $p<0.001$
 Site \times Depth: $F_{14,95} = 0.21$, $p=1.0$
- b) Depth: $F_{7,95} = 0.44$, $p=0.9$
 Site: $F_{2,95} = 69.79$, $p<0.001$
 Site \times Depth: $F_{14,95} = 0.45$, $p=1.0$
- c) Depth: $F_{7,95} = 0.44$, $p=0.9$
 Site: $F_{2,95} = 25.05$, $p<0.001$
 Depth \times Site: $F_{164,95} = 1.23$, $p=0.3$

ANOVA Single cores ($n=1$ at each site) 15-185 cm:

- a) Depth: $F_{16,47} = 0.66$, $p=0.8$
 b) Depth: $F_{16,47} = 1.21$, $p=0.3$
 c) Depth: $F_{16,47} = 0.67$, $p=0.8$

6.3.2 In situ fluxes

6.3.2.1 In situ fluxes of CO₂ and CH₄

CO₂ fluxes did not vary significantly between sites or with depth when the combined data for all sites sampled in July 2008 were analysed (Fig. 6.8a-c). However, in August 2008, CO₂ fluxes (Fig. 6.8d-f) were greatest for the surface horizon at all three sites, ranging from 320-500 mg CO₂ m⁻² h⁻¹. Fluxes from the surface layer were two to three-fold higher than at 30 cm or greater depths and the values were comparable for all sites. The contrasting patterns for CO₂ fluxes between months are reflected by the significant Month×Depth interaction ($F_{3,67}=3.97$; $p<0.05$) resulting from the greatly increased surface efflux in August at the *C. panamensis* and *Cyperus* sp. sites.

There was no significant difference in CH₄ fluxes between sites in July 2008 (Fig. 6.9a-c), although a significant depth effect was found across all three sites, with emissions being greatest 30 cm below the surface. CH₄ fluxes were very low at depths >30 cm at the *R. taedigera* and *C. panamensis* sites, but detectable fluxes were apparent at 60 and 100 cm at the *Cyperus* sp. site. In August 2008, CH₄ fluxes were greatest from the surface layer at the *R. taedigera* and *C. panamensis* sites, while values for the deeper layers were very low (Fig. 6.9d-f). However, no significant variation with depth was found for the *Cyperus* sp. site and the flux from the surface layer was much lower than at the other two sites. The influence of time on the depth distribution of CH₄ fluxes was significant (Month×Depth: $F_{3,76}=5.79$; $p=0.002$).

At the time of sampling in July and August 2008, neither water table nor substrate temperature varied significantly between sites. Cumulative rainfall during the preceding month was also similar, being 322 and 362 mm in July and

August, respectively. The water table tended to be just below the peat surface (average of 8 cm) at the *R. taedigera* site and just above the surface (average of 6 cm) at the two sites closer to the interior of the peatland (Table 6.2). However, rainfall during the 24 h period preceding

sampling rapidly and substantially affected the height of the water table by up to 10-15 cm (Emma Wright, pers. obs.).

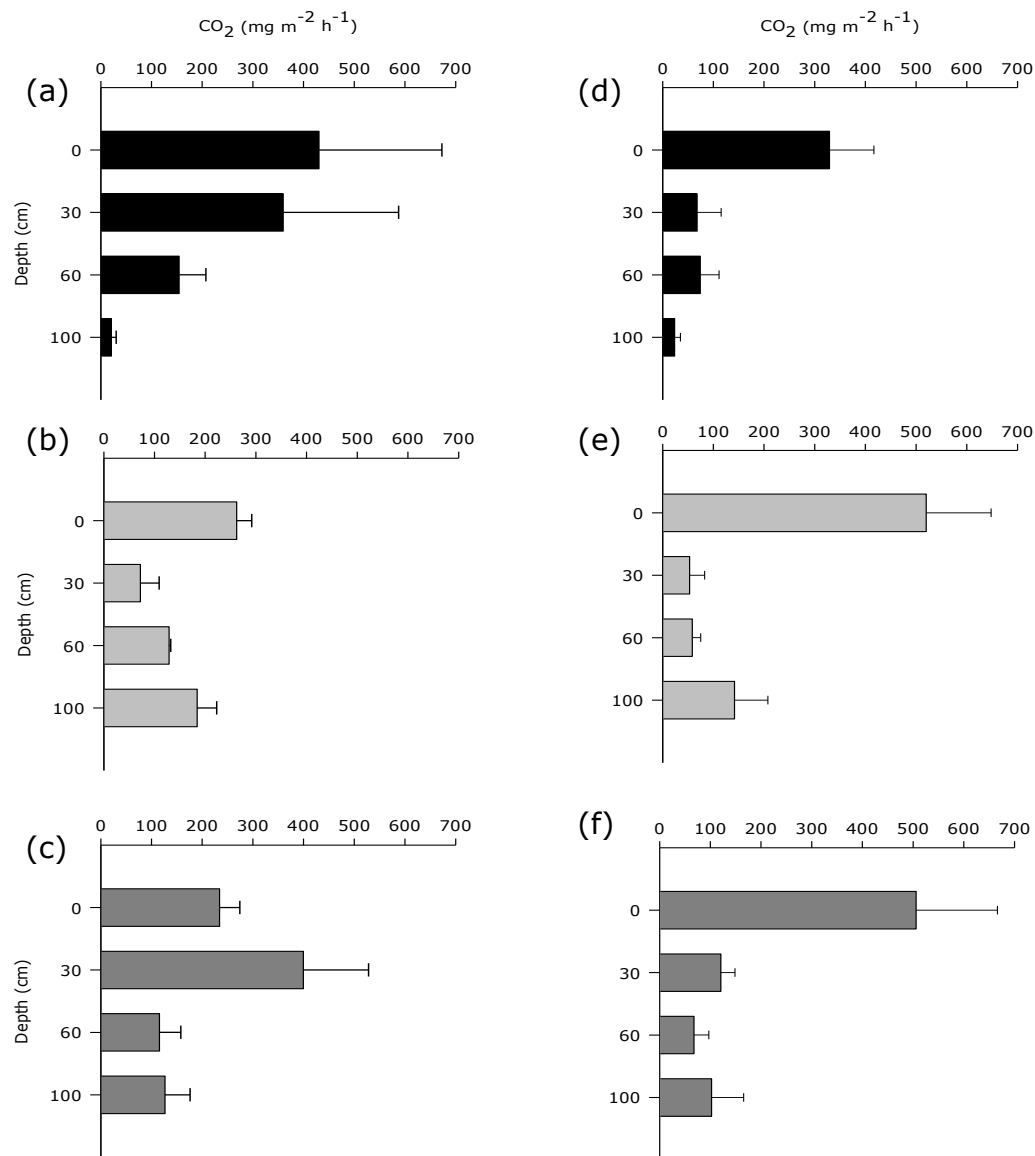


Figure 6.8. Mean *in situ* CO₂ fluxes during July (a-c) and August 2008 (d-f) for a) and d) *R. taedigera*, b) and e) *C. panamensis*, and c) and f) *Cyperus* sp. sites. Fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown (n=4). ANOVA summaries are:

July) Depth: $F_{3,32} = 0.79$, $p = 0.52$
 Site: $F_{2,32} = 0.23$, $p = 0.79$
 August) Depth: $F_{3,42} = 18.43$, $p < 0.001$
 Site: $F_{2,42} = 0.49$, $p = 0.62$

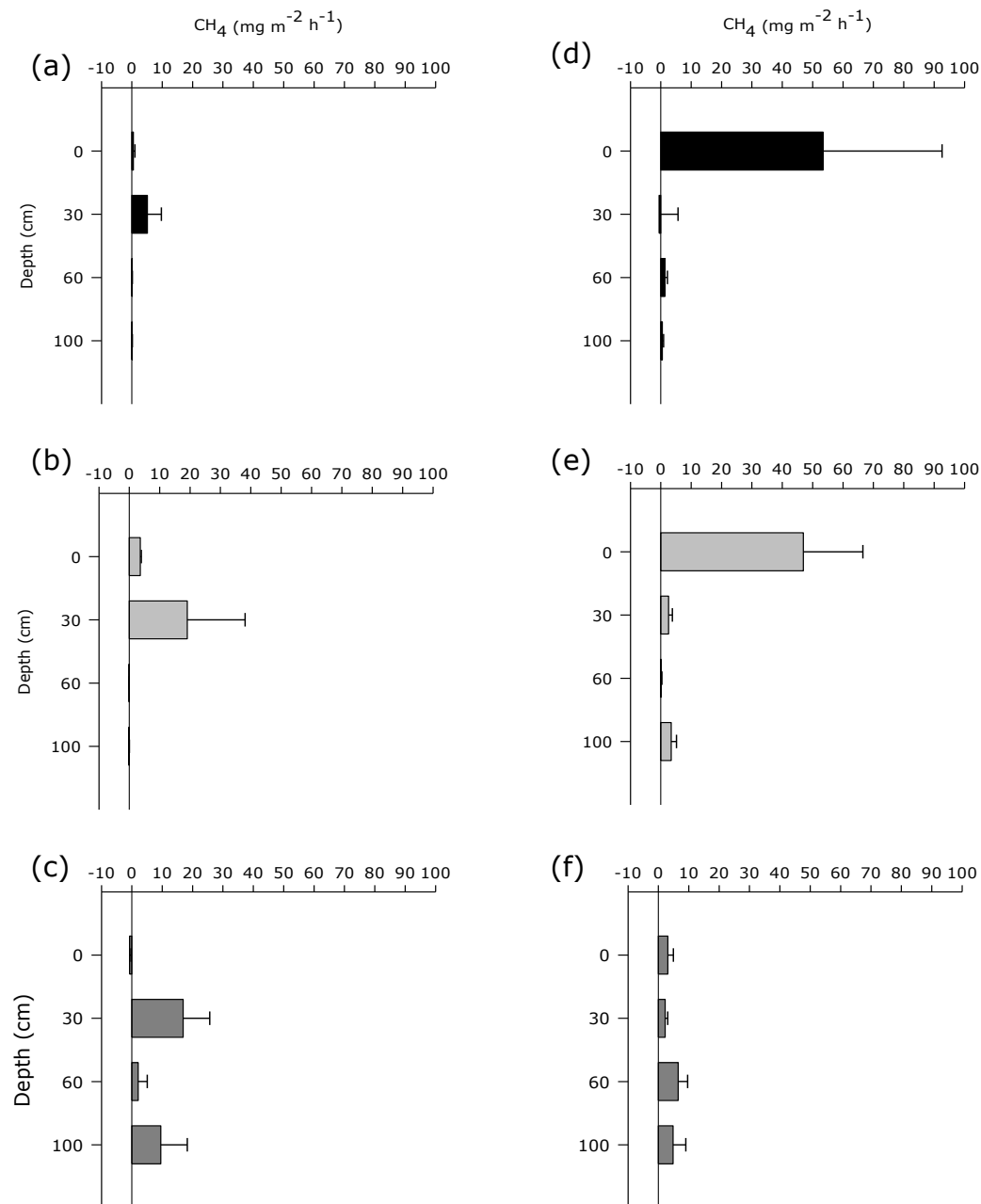


Figure 6.9. Mean *in situ* CH₄ fluxes during July (a-c) and August 2008 (d-f) for a) and d) *R. taedigera*, b) and e) *C. panamensis*, and c) and f) *Cyperus* sp. sites. The fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown (n=4). ANOVA summaries are:

July) Depth: $F_{3,37}=4.55$, $p<0.05$

Site: $F_{2,37}=0.48$, $p=0.6$

August) Depth: $F_{3,46}=6.45$, $p<0.01$

Site: $F_{2,46}=0.37$, $p=0.7$

6.3.3 Ex situ CO₂ and CH₄ emissions

Peat from the *C. panamensis* and *Cyperus* sp. sites tended to respire more rapidly to a depth of c. 70 cm than that from the *R. taedigera* site when expressed on a unit peat mass basis, with a maximum CO₂ production measured at 50 cm depth of 0.12 and 0.08 mg CO₂ g⁻¹ h⁻¹ for the *C. panamensis* and *Cyperus* sp. sites, respectively (Fig. 6.10a). However,

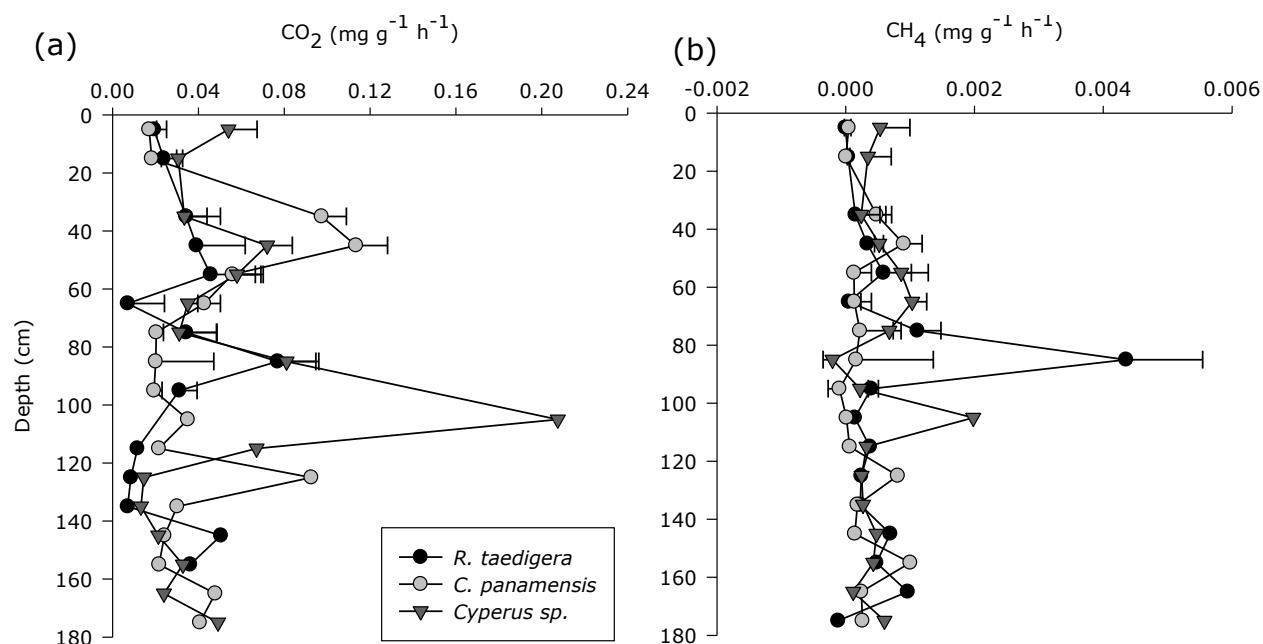


Figure 6.10. Profiles of a) CO₂ fluxes and b) CH₄ fluxes expressed on the basis of peat mass throughout the peat profile. Single standard errors of the mean are shown for depths ≤100 cm (n=5 for 0-10 cm and n=4 for 10-100 cm). Values for depths >100 cm are unreplicated. ANOVA summaries of depths of 5-95 cm were:

a) Depth: $F_{7,83}=3.94$, $p=0.001$

Site: $F_{2,83}=4.00$, $p<0.05$

SitexDepth: $F_{14,83}=3.58$, $p<0.001$

b) Depth: $F_{7,85}=1.51$, $p=0.18$

Site: $F_{2,85}=4.38$, $p<0.05$

SitexDepth: $F_{14,85}=1.36$, $p=0.20$

ANOVA summaries of data 15 - 175 cm (one single core at each site) were:

a) Depth: $F_{17,101}=2.03$, $p<0.05$

b) Depth: $F_{17,101}=21.63$, $p<0.001$

CO₂ production expressed on a unit land area basis was greatest for *R. taedigera*, reflecting the higher bulk density of peat at this site (Fig. 6.11a). CO₂ fluxes peaked at 120-160 cm at all sites, with maximum values of c. 450, 300 and 250 mg CO₂ m⁻² h⁻¹ being obtained for *C. panamensis*, *R. taedigera* and *Cyperus* sp., respectively (Fig. 6.11a).

As for CO₂, CH₄ fluxes expressed on a unit peat mass basis were greater for the *C. panamensis* and *Cyperus* sp. sites at depths of 0-70 cm (Fig. 6.10b; $p < 0.05$), with maximum recorded values of 0.0010 and 0.0012 mg CH₄ g⁻¹ h⁻¹, respectively. By contrast, when expressed per unit land area,

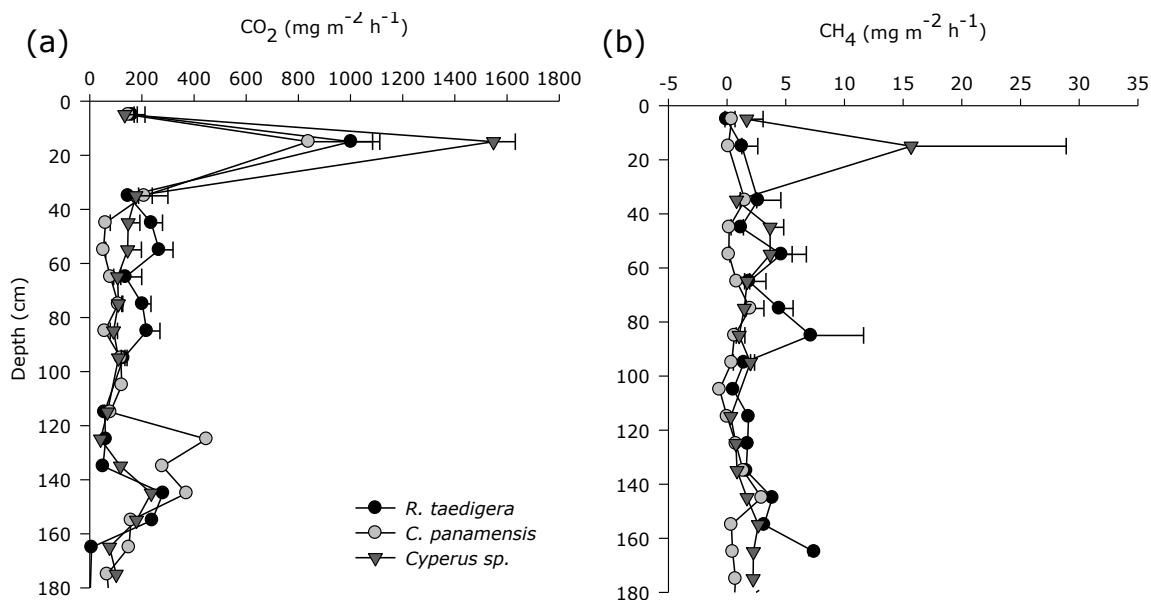


Figure 6.11. Fluxes of a) CO₂ and b) CH₄ expressed on a unit land area basis. throughout the profile. Single standard errors of the mean are shown for depths ≤ 100 cm (n=5 for 0-10 cm and n=4 for 10-100 cm). Values for depths > 100 cm are unreplicated. ANOVA summaries for 5-95 cm are:

- a) Depth: $F_{7,83} = 1.65$, $p = 0.1$
 Site: $F_{2,83} = 10.13$, $p < 0.001$
 Site×Depth: $F_{14,83} = 3.58$, $p < 0.05$
 b) Depth: $F_{7,85} = 1.42$, $p = 0.21$
 Site: $F_{2,85} = 6.29$, $p < 0.01$
 Site×Depth: $F_{14,85} = 1.62$, $p = 0.10$

ANOVA summaries of data 5 – 175 cm (one single core at each site) were:

- a) Depth: $F_{17,105} = 0.96$, $p = 0.5$
 b) Depth: $F_{17,106} = 0.41$, $p = 1.0$

CH₄ fluxes were greater at the *R. taedigera* site for most depths ($p < 0.01$), with a maximum value of c. 7 mg CH₄ m⁻² h⁻¹ being recorded (Fig. 6.11b). CH₄ fluxes were relatively consistent throughout the profile at all sites apart from spikes at depths of 80 cm and 100-110 cm for the *R. taedigera* and *Cyperus* sp. sites, respectively (Fig. 6.11b).

Cumulative CO₂ fluxes (i.e. the sum of fluxes measured from the individual 10 cm segments in the *ex situ* study) to a depth of 2 m (1.6 m for *R. taedigera* due to missing data) were respectively 2995, 2944 and 2156 mg CO₂ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites. Cumulative CH₄ fluxes showed greater variation between sites, being greatest for *R. taedigera* followed by *Cyperus* sp. and *C. panamensis* (47, 29 and 14 mg CH₄ m⁻² h⁻¹, respectively). Cumulative CO₂ and CH₄ fluxes were an order of magnitude greater than the surface fluxes measured at the time of coring. Surface CO₂ and CH₄ fluxes measured at the same sites in November 2007 were 202 ± 46 , 104 ± 54 and 289 ± 44 mg CO₂ m⁻² h⁻¹, and 1.03 ± 0.87 , -0.27 ± 0.39 and 1.12 ± 0.39 mg CH₄ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites, respectively.

Percentage moisture content and bulk density of the peat at each site and depth examined accounted for 33 and 26 % respectively of the variation in CO₂ fluxes (Fig. 8a, b), with CO₂ fluxes being greater for peat with a high moisture content. Bulk density within the peat profile ranged from 0.005-0.102 g cm⁻³, with increased bulk density having a negative effect on CO₂ fluxes in a log linear relationship. In contrast, CH₄ fluxes were not correlated with either moisture content or bulk density (Table 1; $p = 0.11$). Neither Redox potential nor root dry mass had any significant effect on CO₂ (Table 6.2; CO₂ $p = 0.88$; CH₄ $p = 0.91$) or CH₄ fluxes (Table 6.2, CO₂ $p = 0.14$; CH₄ $p = 0.07$).

Variation in pH within the peat had no significant effect on CO₂ flux (Table 6.1; $p = 0.40$), whereas CH₄ efflux was positively correlated with pH ($F_{1,87} = 9.57$; $p = 0.003$). The majority of measurements fell between pH 3.2 and 3.6.

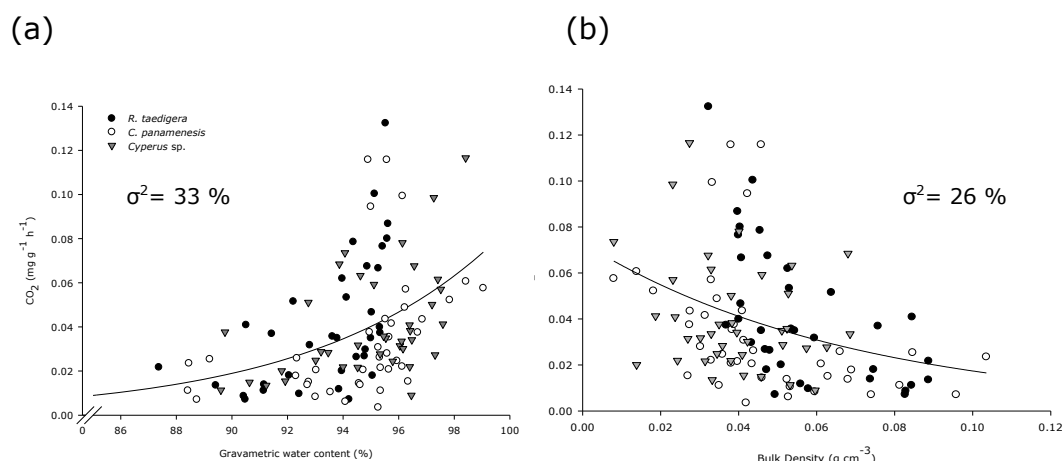


Figure 6.12. Relationship between CO₂ flux and (a) percentage moisture content; $F_{1,114}=58.06$, $p<0.001$ and (b) bulk density of peat ($F_{1,115}=41.14$, $p<0.001$).

CO₂ fluxes showed a significant positive log linear correlation with the organic content (OC) of the peat (Fig. 6.13a; $p<0.001$). The majority of OC values were between 450 and 570 mg C g⁻¹ h⁻¹. A peat with OC content >550 mg C g⁻¹ h⁻¹ was predominantly sourced from the *R. taedigera* site. The variation in OC accounted for 22% of the variation in CO₂ fluxes.

There was a significant linear positive correlation between CO₂ flux and the TN content of the peat (Fig. 6.13b; $p<0.05$). TN values ranged between 10 and 31 mg N g⁻¹ and the *R. taedigera* site is the only one to have values >27 mg N g⁻¹. All values for peat from the *C. panamensis* and *Cyperus sp.* sites were <27 mg N g⁻¹. Variation in TN content accounted for 3 % of the variation in CO₂ fluxes.

There was a significant negative log linear relationship between CO₂ flux and TP (Fig. 6.13c; $p<0.05$), for which c. 60 % of the values were <350 µg P g⁻¹. Over 50 % of the values >400 µg P g⁻¹ were for peat from the *R. taedigera* site. The variation in TP accounted for 6 % of the variation in CO₂ fluxes.

There was a significant positive correlation between CH₄ flux and C:P ratio ($F_{1,115}=5.33$; $p<0.05$). The majority of the values ranged from 500 to

3000 and were fairly evenly distributed across all sites. Variation in C:P ratio accounted for 4 % of the variation in CH₄ fluxes.

No correlations were found between CO₂ or CH₄ fluxes and the ratios of other peat characteristics examined, or with dissolved organic carbon, total phosphorus or total nitrogen concentration in the pore water.

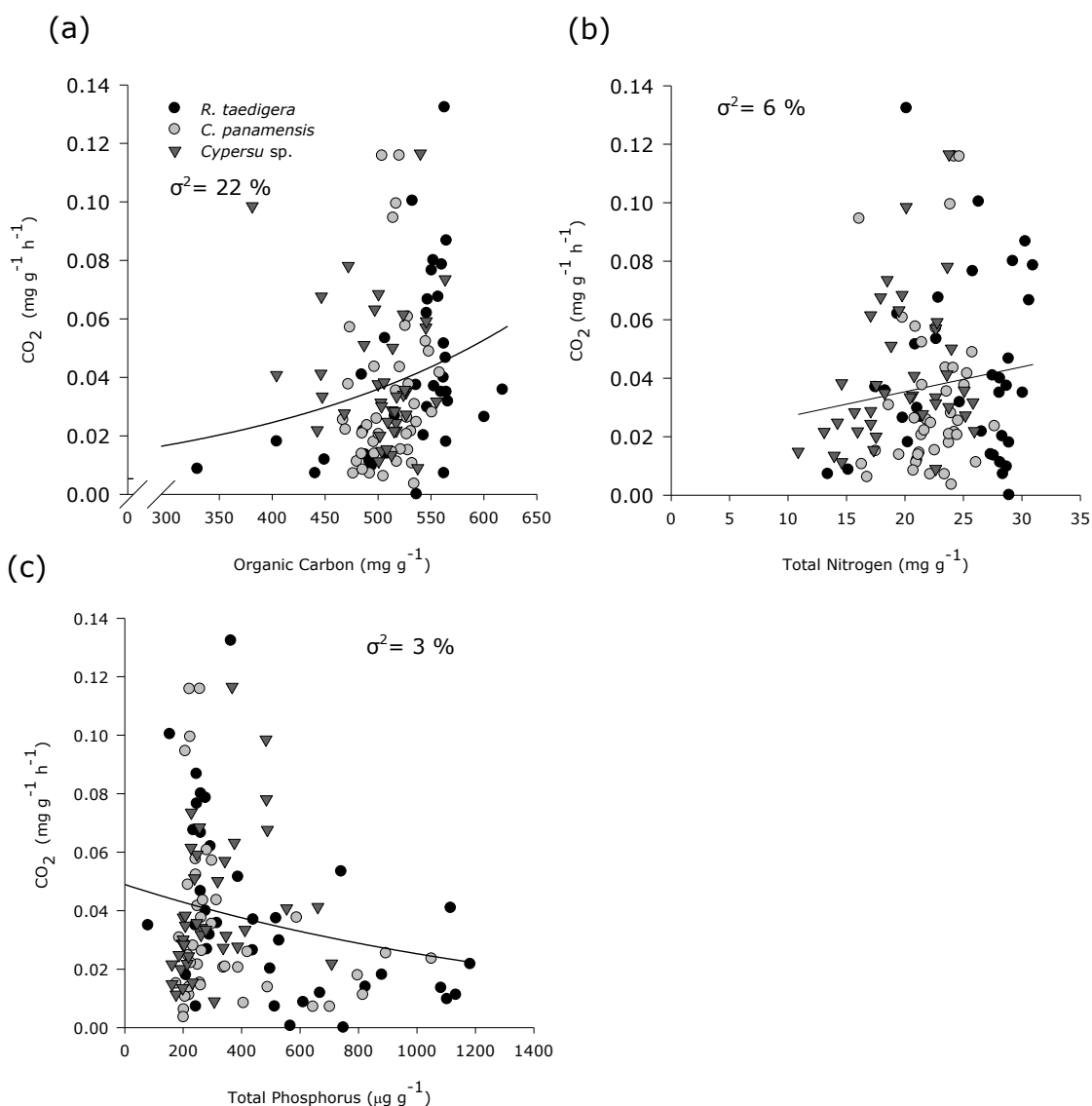


Figure 6.13. Relationship between CO₂ flux and a) organic carbon content (b) total peat nitrogen content and (c) total peat phosphorus content. Regression summaries of data:

a) $F_{1,115}=32.82$, $p<0.001$

b) $F_{1,115}= 7.86$, $p=0.006$

c) $F_{1,121}= 5.32$, $p=0.023$

6.4 Discussion

The *in situ* and *ex situ* measurements both show clearly that the peat layers (from 0 - 2 m) may contribute substantially to the net efflux of CO₂ from the peatland examined here. The *in situ* measurements showed that sub-surface CO₂ production made a greater contribution to net CO₂ emissions from the top 30 cm in August than in July 2008 (Fig. 6.8). This shift in CO₂ emissions suggests the occurrence of strong temporal variability despite the permanently high water table and stable peat temperatures, in sharp contrast to findings in SE Asia where fluctuations in the water table were the main driver of temporal variation in CO₂ fluxes (Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b; Hirano *et al.*, 2007). Measurements extending over longer time periods and with greater temporal resolution are needed to establish the factors controlling temporal variability in CO₂ fluxes in the San San Pond Sak peatland.

The high cumulative CH₄ efflux from the *ex situ* peat cores highlights the potential for substantial emissions of this potent greenhouse gas from tropical peatland, although the relatively low *in situ* net emissions from the peat surface in July, despite substantial production at a depth of 30 cm (Fig. 6.9), suggest strong oxidation of CH₄ in the surface peat. In August, CH₄ emissions from the surface peat were much greater and within the upper range of values reported for SE Asian peatlands (Couwenberg *et al.*, 2010). This suggests that the peatland can switch rapidly from being a weak to a strong source of CH₄ and highlights that, as for CO₂, strong variation in CH₄ emission can occur without variation in the water table or peat temperature. The depth distribution of CO₂ and CH₄ fluxes did not vary greatly among sites, suggesting that gas production does not depend directly on the properties of distinct vegetation communities, such as the nutrient status of the litter produced (Troxler, 2007; Sjögersten *et al.*, 2010).

The large *ex situ* gas fluxes relative to the *in situ* fluxes may well reflect the slow gas diffusion through the water-saturated peat profile *in situ*. High gas concentrations at depth in peat profiles have been recorded

previously in tropical peatlands (e.g. Inbushi *et al.*, 1998; Melling *et al.*, 2005 a). The *ex situ* fluxes reported here should therefore be interpreted as potential fluxes following removal of the hydraulic head, rather than a measure of the actual contribution of individual peat layers to surface emissions. The release of CH₄ from deep peat layers to the atmosphere is likely to be mediated both by the dominant vegetation (Joabsson *et al.*, 2001) and ebullition, which is known to be an important transport mechanism for the release of CH₄ in northern peatlands (Comas *et al.*, 2007).

The high *in situ* CO₂ fluxes in August suggest substantial losses of C from the peatland if extrapolated to an annual timescale. Such large C losses must be balanced by similarly high gross net primary productivity to maintain the C accumulation rates estimated by Phillips *et al.* (1997). High tree basal areas have been reported for the *R. taedigera* and *C. panamensis* sites (Sjögersten *et al.*, 2010), but further work on their productivity and carbon allocation is needed to determine the C balance of the peatland. Indeed, substantial below-ground C inputs of labile carbon from the trees might be an important contributor to the high *in situ* CO₂ and CH₄ fluxes, analogous to the reports of strong direct controls of gas production by the vegetation in northern peatlands (Joabsson *et al.*, 2001).

The OC, TN and TP content of the peat varied with site and had significant effects on the CO₂ efflux (Fig. 6.13). The carbon and nutrient content of the peat is initially influenced by the quality of the fresh litter inputs. The organic composition of the peat varied between sites as determined using solid state ¹³C CPMAS NMR spectroscopy to determine the proportions of aliphatic, carbohydrate and aromatic carbon (*cf.* Appendix A). The results demonstrated that a large proportion of the variance in CO₂ and CH₄ production could be related to the quantity of carbohydrates in the peat (30 and 63 % respectively), but that gas production through the peat profile was regulated in part by the degree of decomposition of the peat. The carbohydrate concentration of the peat may therefore limit the responses of CO₂ and CH₄ production to climatic change. Although the

peat appears to be more susceptible to decomposition at the *C. panamensis* and *Cyperus* sites, the *R. taedigera* site exhibited the greatest cumulative CO₂ and CH₄ emissions per unit land area to a depth of c. 2 m due to the slightly greater density of the peat.

The ratios of peat carbon and nutrient contents varied with depth (Fig. 6.6), with lower ratios in the surface horizons suggesting that carbon and nutrients become increasingly limiting with depth for the production of CO₂ and CH₄ (Bedford *et al.*, 1999; Sjogersten *et al.*, 2010).

With respect to the relationships between CO₂ fluxes, bulk density and soil moisture content (Fig. 6.12), we speculate that these reflect to some extent either substrate lability, i.e. the relatively low density peat at the *Cyperus* site tended to be more carbohydrate-rich, or that supplies of O₂ and labile DOC (Charman *et al.*, 1994) to depth through highly permeable peat stimulated respiration. However, the measured profiles for DOC (Fig. 6.7a) did not provide reliable predictions of gas production. The density of peat was generally low and within the range reported for tropical peatlands (Shimada *et al.*, 2001; Page *et al.*, 2004; Lahteenoja *et al.*, 2009). It is also interesting to note that bulk density did not change consistently with depth to 2 m. Similarly, bulk density was low throughout the profile in peatlands in Kalimantan to a depth of 9 m and in some peats in the Amazon to depths of 4.9 m (Page *et al.*, 2004; Lahteenoja *et al.*, 2009). These observations suggest that low bulk density may be an important feature of tropical peatlands compared to the denser peat found at depth in temperate and boreal peatlands (Laiho *et al.*, 2004; Danevcic *et al.*, 2010).

Redox potential did not explain the variation in CO₂ and CH₄ fluxes from peat cores from the San San Pond Sak peatland. Similarly, spatial variation in CO₂ and CH₄ fluxes under field conditions have been found to be independent of redox potential (Ueda *et al.*, 2000; Chimner & Ewel, 2004; Hadi *et al.*, 2005), suggesting that other soil properties, such as nutrient status, are more important drivers (Wright & Reddy, 2001; Hadi

et al., 2005; Yu *et al.*, 2007). However, the relatively high redox potentials observed throughout the profile to a depth of 2 m and the high root biomass down to c. 110 cm (Fig. 6.4) may have been at least partly responsible for the large gas production in the sub-surface peat (Figs. 6.4, 6.10, 6.11; Bergman *et al.*, 1999; Metcalfe *et al.*, 2007; Yu *et al.*, 2007, Seo and Dehaune 2010).

Climate change predictions for Panama suggest an increase in air temperature of up to 3.5 °C and a reduction in precipitation (Meehl *et al.*, 2007), potentially lowering water tables in the peatland. As water table draw-down has been shown to increase CO₂ emissions SE Asian peatlands (Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009), it is plausible that any reduction in water table resulting from climate change would increase CO₂ emissions from San San Pond Sak, a view supported by the increased CO₂ fluxes from experimentally drained surface peat from the site (Sjögersten *et al.*, 2010). The potential fluxes of CO₂ and CH₄ to a depth of 2 m (Fig. 6.10) suggest that the deeper layers of peatlands may contribute substantially to increased CO₂ and CH₄ emissions in response to elevated temperature (Hirano *et al.*, 2009; Long *et al.*, 2010). Draw-down of the water table would reduce the extent of the anaerobic micro-sites in the upper 30 cm of the peat profile which currently are most active in producing CH₄ (Fig. 6.9). The combined effect of the lower quality of peat at depth (Table 6.1) and a thicker surface layer of aerated peat where oxidation of CH₄ takes place would be likely to reduce CH₄ emissions from this neotropical peatland.

In conclusion, detailed knowledge of the processes affecting gas production from deep peat layers is essential to predict how climate change may affect the net fluxes of CO₂ and CH₄ from tropical peatlands. Moreover, it is clear that deeper peat layers have the potential to lose C rapidly, and that variation in peat quality and bulk density within the profile associated with contrasting vegetation communities in tropical peatland is important in determining CO₂ and CH₄ production. There is currently a dearth of information regarding the sources of CO₂ and CH₄ within peat profiles, the environmental constraints to the release of the

gases produced and the influence of vegetation type on both the production and release of these gases. Further work including radiocarbon dating of DOC, CO₂ and CH₄ gases and more intensive measurements of gas emissions in relation to the role of the vegetation and abiotic variables is needed to fill the knowledge gaps which currently limit our ability to predict CO₂ and CH₄ emissions from neotropical peatlands. Such studies are vital in view of the substantial land areas occupied by such systems and their considerable potential contribution to future climate change

Chapter 7. Nutrient cycling at three sites in the San San Pond Sak wetland, Panama

7.1 Introduction

7.1.1 Factors influencing litter decomposition

Wetland plants have an important role in the carbon cycle of peatlands as they are a significant carbon sink *via* inputs of fresh litter to the peat surface, and also within the profile as decaying roots and root exudates (Kao *et al.*, 2003; Chimner and Ewel, 2005; Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009). The slow decomposition of litter in wetlands due to waterlogging is the primary cause of accumulation of peat and the role of wetlands as a potential carbon sink (Bernal and Mitsch, 2008; Zhang *et al.*, 2008; Kayranli *et al.*, 2010). Vegetation inputs to the peat are degraded either aerobically to produce CO₂ or anaerobically to produce CH₄. Aerobic decomposition is generally more rapid than anaerobic decomposition (Wright and Reddy, 2001). Several environmental factors affect decomposition rate in wetlands, including soil temperature, moisture content and litter quality.

Increases in soil temperature generally increase decomposition rates, as is clearly illustrated by northern and boreal wetlands which experience strong seasonal shifts in temperature (Kadlec and Reddy, 2001; Guo *et al.*, 2008). In contrast, wetlands in tropical regions experience more consistent temperatures throughout the annual cycle (Grisi, 1997; Waddington *et al.*, 1998; Joiner *et al.*, 1999; Hashimoto *et al.*, 2003; Jauhiainen *et al.*, 2005). Although some tropical wetlands experience extreme wet and dry seasons and a greater range of soil temperature, these are the exception rather than the norm (Adachi *et al.*, 2009).

The moisture content of peat is linked to rainfall and the level of the water table, an important factor in all types of wetland. However, tropical regions generally have pronounced wet and dry seasons, with potential effects on the level of the water table. This is important because draw-down of the water table increases aeration of the surface peat layers, thereby allowing aerobic decomposition to occur (Schwendenmann *et al.*, 2003; Jauhiainen *et al.*, 2005). When the water table reaches the peat surface, the consequent waterlogged conditions suppress aerobic decomposition and limit decomposition rate (Miyajima *et al.*, 1997; Wright and Reddy, 2001; Battle and Golladay, 2007). The timing of rainfall events is also important as some studies have reported that alternating cycles of wetting and drying of the surface material create ideal moisture conditions for decomposition (Battle and Golladay, 2007; Guo, 2008).

The quality of fresh litter inputs to the peat surface may also affect degradation rate as litter from different plant species varies in its composition and decomposability (Miyajima *et al.*, 1997; Guo *et al.*, 2008; Yule and Gomez, 2009). Thus, litter containing a greater proportion of easily degradable material may increase the rate of decomposition compared to species containing more recalcitrant material (Kao, 2003; de Neff *et al.*, 2006; Crawford *et al.*, 2007). Litter of lower quality may also decrease decomposition rate through nutrient limitation (Fennessy *et al.*, 2008; Wang *et al.*, 2010), which can control forest composition and microbial processes within the peat (Sjogersten *et al.*, 2010). Potentially the quantity of litter inputs may also influence decomposition, as a greater quantity of litter will potentially equate to a greater supply of labile material.

In addition to environmental factors influencing the rate of decomposition processes, extracellular enzymes produced by microbes are crucial to the decomposition of organic matter. The production of extracellular enzymes is affected by several factors including temperature, substrate availability and quality, degree of soil aeration and moisture content. Surface vegetation affects the substrate availability and quality and also the degree of soil aeration through fresh litter inputs and root inputs (exudates, O₂ and dead roots), with implications for enzyme activities (Freeman *et al.*, 2004; Choi *et al.*, 2009). Fresh litter inputs can either enhance the production of extracellular enzymes and increase decomposition (e.g. Choi *et al.*, 2009; Jackson *et al.*, 2009) due to increased nutrient availability; alternatively, enzyme activity may decrease when nutrient availability is increased (e.g. Sinsabaugh *et al.*, 1993). Enzyme activity in wetlands is generally greatest in the surface layer, where fresh litter inputs are received, and decreases with depth (A. Cheesman, unpublished data; Wright *et al.*, 2001; Jackson *et al.*, 2009). Deeper peat is formed of partially decomposed, recalcitrant material and is typically nutrient-poor.

The dominant vegetation species in the peatland system investigated here, San San Pond Sak, show distinct variation along a nutrient gradient (Phillips *et al.*, 1997; Troxler *et al.*, 2007; Sjogersten *et al.*, 2010; *cf.* Section 2.1 for site description). As substrate temperature varies little during the annual cycle (data from Bocas del Toro weather monitoring station), the present study focussed on the influence of litter and peat quality and the level of the water table on decomposition processes.

Laboratory incubations were carried out using litter and peat from the San San Pond Sak wetland to test the hypotheses that:

- 1) Litter from sites dominated by *R. taedigera*, *C. panamensis* and *Cyperus* sp. decomposes at different rates which reflect the bioavailability of C, N and P in the litter.
- 2) Decomposition is most rapid when the water table is low and nutrient loading decreases extracellular microbial enzyme activity at all sites, with the greatest effect being seen at the nutrient-poor *Cyperus* sp. site.

7.2 Materials and Methods

7.2.1 Loss of litter mass under high and low water tables

To determine the role of leaf litter input to peat formation under different vegetation communities, long term litter mass loss rates were determined for the dominant litter types at three sites in the San San Pond Sak wetland. Standing dead leaf litter (dead material still attached to the plant) was collected from the *R. taedigera* and *Cyperus* sp. sites and newly fallen dry litter was collected from the *C. panamensis* site. The state of the litter therefore reflected its condition when it is about to be incorporated into the peat. Approximately 2 kg of litter was collected from each site, air-dried and shipped to the University of Nottingham, where it was cut into pieces c. 1.5 x 1.5 cm in area and homogenised. Ninety samples, each with a mass of 1.5 g, were weighed out for both *R. taedigera* and *C. panamensis* litter; a further 90 samples of litter from the *Cyperus* sp. site, each weighing 1.0 g, were used to provide samples of similar volume. Each sample was placed in a fine nylon bag (10 × 10 cm) with a mesh diameter of c. 1 mm and tied with nylon thread before attaching uniquely numbered plastic identification labels.

Material from each site was sub-divided into three groups, each containing 30 replicate samples, and placed in plastic trays containing a 3 cm deep layer of sand. A 100 ml aliquot of distilled water and 10 g of peat from the relevant field site was thoroughly mixed with the sand before placing fine nylon material mesh (mesh diameter c. 1 mm) over the sand. Distilled water was added to provide two treatments: 1) sand was fully wetted with no surface pooling and 2) water level was 5 cm above the sand surface. These water tables were chosen to simulate saturated and flooded field conditions; these are defined as the 'low' and 'high' water table treatments.

The samples were placed in incubators at 30 °C and five randomly selected litter bags from each site and experimental treatment were sampled after 1, 2, 3, 9, 13 and 15 months, air-dried and weighed before being ashed at 550 °C for 3 h. The remaining organic matter was calculated as a percentage of the original organic matter content based on the initial litter sample weight.

7.2.2 Litter degradation and change in nutrient content

To determine the rate of release of nutrients from the litter, a further experiment was carried out using litter samples collected, air dried and shipped to the University of Nottingham as described in Section 6.2.1. 50 samples each weighing 3.5 g were placed in 10 x 10 cm mesh bags for the *R. taedigera* and *C. panamensis* sites, while 50 samples each weighing 1.0 g were used for the *Cyperus* sp. site.

Trays were set up containing a 2 cm thick layer of foam sponge in the base of the tray to simulate peat; the sponges were soaked for 24 h in distilled water and squeezed before adding to trays to

remove water soluble contaminants from the sponges. The litter bags were placed on the sponges before adding a suspension of distilled water and soil microbes from each of the sites examined and applying two water table depths. These treatments were defined as flooded, where the water table was 5 cm above the sponge surface, and saturated where the water table was at the surface of the sponge (analogous to the treatments in the long term decomposition experiment described above). For the trays simulating flooded conditions, the sponges were soaked in de-ionised water and placed on top of the samples, whereas dry sponges were placed over the litter bags to simulate dry conditions. These treatments simulated flooded (water table above the surface, defined as 'high water table') and saturated (water table at the surface, defined as 'low water table') field conditions. The trays containing the litter bags were placed in incubators at 30 °C and water levels were maintained. Five randomly selected samples were air-dried and weighed for each litter type and water table combination at the end of Weeks 1, 2, 4, 8 and 12.

Three extraction procedures were used to determine the lability of carbon (C), nitrogen (N) and phosphorus (P) within the litter. Water extraction was used to estimate the size of the most labile fraction (e.g. sugars, amino acids, DNA), followed by acid extraction to determine substances of intermediate lability (e.g. hemicellulose and cellulose). The non-acid-extractable residual fraction was considered to reflect the recalcitrant portion of the litter (lignin and long chain aliphatic molecules). To determine how the water table treatments impacted on litter chemistry, C, N and P concentrations were determined in each fraction for samples collected after 1 and 12 weeks of incubation.

To achieve this, air-dried samples were ground to fine powder using a ball mill before placing 1 g sub-samples of *R. taedigera* and *C. panamensis* material and 0.5 g samples of *Cyperus* sp. material in 25 ml capacity screw-top plastic tubes. 20 ml of milliQ water was added to each sample before sealing the tubes. The samples were placed in a water bath at 30 °C with a shaking speed 100 rpm for 12 h before being filtered through pre-weighed Whatman number 50 filter papers; 10 ml of milliQ water was used to rinse out the sample tubes prior to further filtration. Used filters were placed overnight in a drying oven at 80 °C to dry before further processing.

Sample filtrate was placed in 25 ml screw top tubes and stored at 4 °C prior to analysis for dissolved organic carbon (DOC) and total nitrogen (TN) using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). Total phosphorus (TP) was measured using standard molybdate spectroscopy with an absorbance wavelength of 880 nm.

The oven-dried (80 °C) filters were weighed to determine the weight of the remaining litter fraction and the dried samples weighed transferred to 20 ml volume Teflon digest containers at rates of 0.5 g for *R. taedigera* and *C. panamensis* and 0.25 g for the *Cyperus* sp. site. 20 ml of 6 M hydrochloric acid (HCl) was added to each digest container and the top loosely applied. The samples were then placed on a hot plate in a fume hood at 116 °C for 16 h before being filtered using pre-weighed Whatman number 50 filter paper. The digest containers were rinsed with 10 ml of milliQ water before placing the filter papers in an oven at 80 °C overnight to dry. The filtrate was analysed for DOC, TN and TP using the protocols described above. The dried filters were weighed to record the mass of litter remaining. The dried residue from the acid extraction was analysed to determine total carbon (TC), nitrogen (TN) and phosphorus (TP). TC and TN were analysed using a CNS total

element analyser (Flash EA 1112 Series, CE Instruments Ltd, UK). TP was analysed by ashing 0.2 g of acid residue samples for *R. taedigera* and *C. panamensis* and 0.1 g of sample for the *Cyperus* sp. site at 550 °C for 3 h; different quantities of material were used due to the differing availability of remaining litter. The ashed material was weighed before being placed in a screw top tube with 20 ml of 1 M H₂SO₄ for *R. taedigera* and *C. panamensis* and 10 ml for *Cyperus* sp to provide a ratio of 10 ml of acid per 0.1 g of sample) and shaken for 24 h. The solutions were allowed to settle before removing and analysing the supernatant for TP using molybdate spectroscopy and the standard protocol outlined above. Included in the extraction procedure were five 'initial' samples of each litter type to provide a measure of the original C, N and P quantities in each of the extracted fractions.

7.2.3 Enzyme assays to determine effect of nutrient amendments

The activity of five enzymes (phosphomonoesterase, phosphodiesterase, β -glucosidase, cellobiohydrolase and β -xylanase) after nutrient amendments of peat samples (*cf.* Section 4.2.3 for nutrient amendment protocol) from the three sites examined were measured. These enzymes are involved in the decomposition of litter and nutrient release within peat. The activity of phosphomonoesterase and phosphodiesterase were measured as these enzyme are involved in the release of P from plant material and would be expected to be high in systems that are P-limited as San San Pond Sak has been found to be (Sjogersten *et al.*, 2011; Wright *et al.*, 2011). Cellobiohydrolase catalyses the breakdown of cellulose, the products of which are then hydrolysed by β -glucosidase to form glucose. Both of these enzymes are involved in the breakdown of labile material and as such would be expected to

have higher activity rates when the concentration of labile substrate is higher. β -xylanase catalyses the breakdown of hemicellulose, a component of plant cell walls, as such the activity rate of this enzyme is expected to be higher when there is a higher availability of hemicellulose (semi-labile substrate).

Nutrient amendments were applied to the peat samples by adding 5 ml of either a 2500 mg l⁻¹ (high) or 250 mg l⁻¹ (low) solution. This was equivalent to an addition rate of 0.1 or 0.01 mg g⁻¹ peat (dry weight basis). Mean dissolved nitrogen concentrations in the peat surface water were 2, 16 and 7 mg l⁻¹ at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites respectively. Mean dissolved phosphorus concentrations in the water within the surface peat were 0.20, 0.18 and 0.01 mg l⁻¹ at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites respectively (cf. Section 4.3.1).

A methylumbelliferone-linked fluorogenic substrates (Marx *et al.*, 2001) protocol was used to measure enzyme activity for five enzymes and substrates:

- (1) Phosphomonoesterase (4-methylumbelliferyl phosphate)
- (2) Phosphodiesterase (bis-(4-methylumbelliferyl) phosphate)
- (3) β -glucosidase (4-methylumbelliferyl β -D-glucopyranoside)
- (4) Cellobiohydrolase (4-methylumbelliferyl β -D-cellobiopyranoside)
- (5) β -xylanase (4-methylumbelliferyl β -D-xylopyranoside)

Samples were frozen for up to two weeks before being transferred to a refrigerator at 4 °C overnight prior to analysis. 200 ml of 1 mM NaN₃ was added to each 2 g sample (dry weight basis) of peat and stirred for 15 min. 50 μ l of the resulting soil suspension was then pipetted into a 96-well microplate prepared to contain 100 μ l of a 200 μ M substrate to provide a concentration of 100 μ M, followed by 50 μ l of sodium acetate-acetic acid buffer (adjusted to pH 5). Microplates were then incubated at 27 °C for 40 min. Following

incubation, 50 μ l of 0.5 M NaOH was added to each well to terminate the reaction and analysed immediately using a fluostar Optima spectrofluometer (BMG Habtech, Offenbury, Germany).

7.2.4 Data analysis

The two litter decomposition studies were analysed statistically using analysis of variance (ANOVA) carried out in a two stages. In the first set of analyses, 'litter type', 'WT treatment', 'sample removal time' and their interactions were used as factors, with the mass loss of the litter samples and C, N and P concentrations following the three extraction procedures as the response variables. Secondly, each litter type was tested separately using ANOVA to establish any effects on mass loss of 'WT treatment', 'sample removal time' and their interactions.

The effects on the extracellular microbial enzyme activity of the peat were firstly tested on an overall basis with all peat types included. An unbalanced ANOVA was performed due to the high root biomass in the surface peat at the *Cyperus* sp. site (*cf.* Section 6.3.1.1); as the mass of peat collected was less than that of the other sites only six replicates were used compared to the eight replicates for *R. taedigera* and *C. panamensis* sites. 'Nutrient amendment', 'peat source site' and their interactions were used as factors in the model, with the different enzyme activities as the response variable. Secondly, the effect of high and low nutrient amendments relative to the controls for each individual peat types were analysed using an unbalanced ANOVA for each enzyme e.g. the effect of low/high N additions on phosphomonoesterase activity within peat from the *R. taedigera* site. The effects of temperature on extracellular enzyme activity were tested using an unbalanced

ANOVA of the control group to establish effects of 'temperature' and 'peat source site' and their interactions.

All statistical analysis was performed using Genstat version 10.1 (Lawes Agricultural Trust, Rothamsted Experimental Station).

7.3 Results

7.3.1 Influence of water table on loss of litter mass

All litter types lost mass with time (Figs. 7.1 a, b, c; $F_{2,171}=224.88$, $p<0.001$). *C. panamensis* litter showed the greatest mean mass loss of organic matter (OM) (40 % after 15 months), followed by *Cyperus* sp. (30 %) and *R. taedigera* (19 %). *R. taedigera* litter showed a greater initial OM loss in the high WT treatment than in the low WT treatment (Fig. 7.1a). This continued until the fifth sampling date (23 October 2009), after which mass loss was greater under low WT than under the high WT. *C. panamensis* consistently showed the greater mass loss in the low WT treatment and also had the greatest initial OM losses under both high (29 %) and low (39 %) WTs than the other litter types (Fig. 7.1b, e). After the initial high losses, decomposition rates had decreased dramatically after approximately two months of incubation ($<0.05\% \text{ d}^{-1}$) and remained low for the rest of the study. This decrease following the initial rapid decomposition rate was observed for all litter types and WT treatments except with the exception of *R. taedigera* litter in the low WT treatment, which exhibited the greatest decomposition rate after three weeks of incubation. *Cyperus* sp. litter also showed a greater initial mass loss in the high WT treatment than in the low WT treatment (Fig. 7.1c, f); however, in contrast to *R. taedigera*, mass loss for *Cyperus* sp. litter

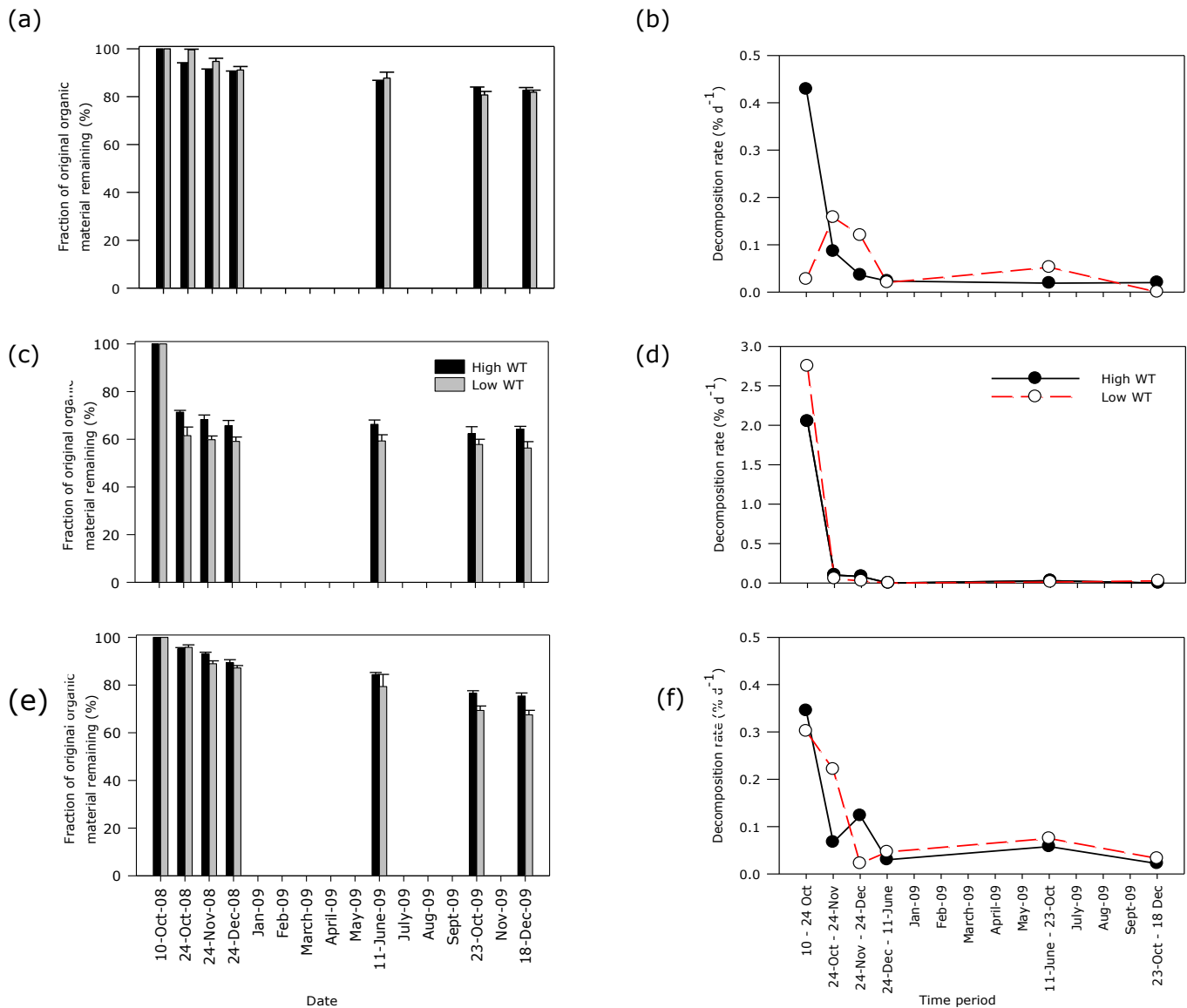


Figure 7.1. Change in mass of litter expressed as percentage of the original organic material remaining at the time of sampling for a) *R. taedigera*, b) *C. panamensis* and c) *Cyperus* sp. for two water table (WT) depths; High WT corresponds to 5 cm above the surface and Low WT is wet to the surface but with no pooling. Single positive standard errors of the mean are shown (n=5 replicates). Mean litter decomposition rates are also shown for d) *R. taedigera*, e) *C. panamensis* and f) *Cyperus* sp. Note the different scale for the rate of litter decomposition for *C. panamensis*. ANOVA summaries;

- a) Treatment: $F_{1,55} = 1.12$, $p = 0.3$
Time: $F_{5,55} = 101.3$, $p < 0.001$
Time x Treatment: $F_{5,55} = 9.02$, $p < 0.05$
- b) Treatment: $F_{1,57} = 8.61$, $p < 0.05$
Time: $F_{5,57} = 3.71$, $p < 0.05$
Time x Treatment: $F_{5,57} = 0.58$, $p = 0.6$
- c) Treatment: $F_{1,57} = 15.37$, $p < 0.005$
Time: $F_{5,57} = 52.11$, $p < 0.001$
Time x Treatment: $F_{5,57} = 1.45$, $p = 0.3$

in the low WT treatment exceeded that under high WT after three weeks of incubation.

After seven weeks of incubation, decomposition rates had decreased from the initial high rates and were generally greatest for *Cyperus* sp. litter in both WT treatments.

7.3.2 Influence of nutrient status on litter decomposition

7.3.2.1 Total initial composition of litter samples

The carbon (C) content of litter before decomposition was similar for *R. taedigera* and *C. panamensis* at c. 60 % (Fig. 7.2) slightly lower than in *Cyperus* sp. (65 %), in which the higher C content was attributable mainly to the acid extractable (semi-labile) component (12 %) compared to 9 and 7 % respectively for *R. taedigera* and *C. panamensis*. Water extractable (labile) C content was similar in all litter types at c. 1 %, as was the recalcitrant residual C content (c. 50 %). Overall there was marginally more labile and semi-labile C in *Cyperus* sp. litter than in that from *R. taedigera* and *C. panamensis*.

Total nitrogen (N) content was similar for all litter types at c. 2 % (Fig. 7.2). The smallest initial labile N content was found in litter from *R. taedigera*, (0.02 %) compared to 0.05 and 0.06 % respectively in *C. panamensis* and *Cyperus* sp. However, semi-labile N content was greatest in litter from *R. taedigera* (0.7 %) followed by *C. panamensis* (0.5 %) and *Cyperus* sp. (0.4 %). Recalcitrant N content was similar in all three litter types, being 1.3 % in litter from *R. taedigera* and *C. panamensis* and 1.4 % in *Cyperus* sp.

The initial phosphorus (P) content differed between litter types. Total P content in *R. taedigera* was 0.014 %, of which 0.013 % was held in the labile and semi-labile fractions and <0.001% was held in the recalcitrant fraction. *C. panamensis* had the next highest total P content of 0.09 %, of which the majority was held in either the labile or semi-labile fractions and <0.001 % in the recalcitrant fraction. *Cyperus* sp. had the lowest total P content of 0.004 %, of which <0.001 % P was in the recalcitrant fraction.

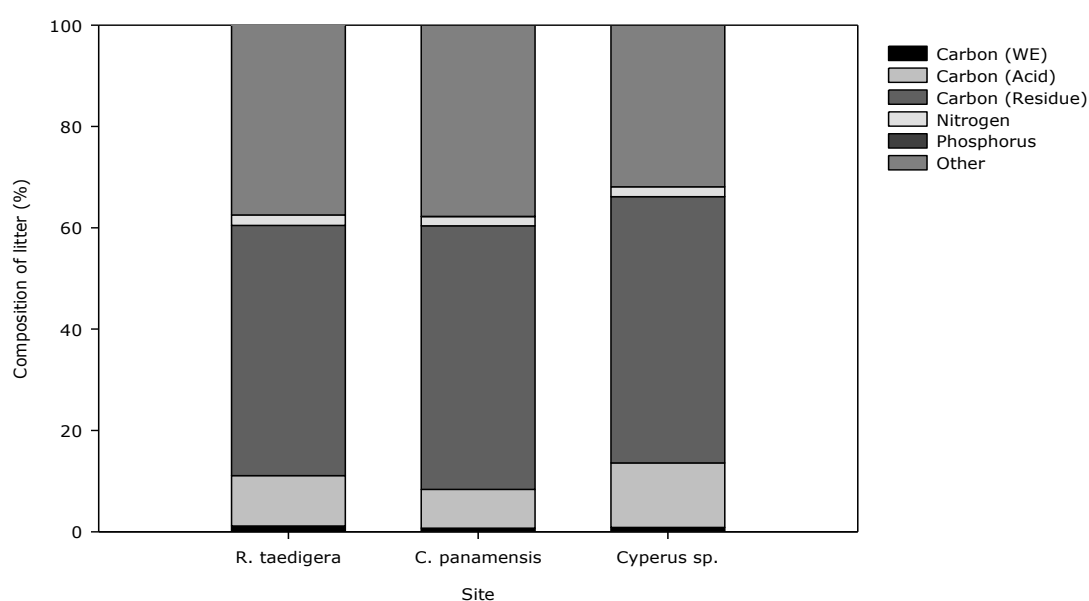


Figure 7.2. Initial composition of *R. taedigera*, *C. panamensis* and *Cyperus* sp litter before incubation. Carbon is shown as percentage water extractable, acid extractable and residual whereas the values for nitrogen and phosphorus show the total percentage extractable by all processes.

7.3.2.2 Influence of two water table treatments on labile, intermediately-labile and recalcitrant C, N and P for three litter types

7.3.2.2.1 Water extractable C, N and P

Water extractable C concentrations were significantly affected by litter type, sampling time and water table (Fig. 7.3a, b; Table 7.1). Mean C concentrations were slightly greater for *R. taedigera* litter than that of *C. panamensis* and *Cyperus* sp. Carbon concentrations in Week 1 were significantly lower than in Week 0, but showed no further significant change between Weeks 1 and 12. The water table treatments differed significantly, with C concentrations being higher under low WT. There were significant litter type x water table interactions ($F_{2,57}=4.68$, $p<0.05$) as C values were similar in all litter types under high WT conditions. However, under low WT conditions the C concentrations of litter were greater for *R. taedigera* than for *C. panamensis* and *Cyperus* sp., for which the values were similar. The Time x water table interaction was significant ($F_{1,57}=7.14$, $p<0.05$) as C concentrations were similar in the high WT treatment at Week 1 and 12, whereas the values were significantly greater at Week 12 than Week 1 in the low WT treatment.

Water-extractable N concentrations were significantly affected by litter type, time and WT treatment (Fig. 7.3c, d; Table 7.1). Extractable N concentrations were greatest for *Cyperus* sp. and similar for *R. taedigera* and *C. panamensis*. N concentrations generally increased over time, with the greatest increase occurring between Weeks 1 and 12. There was a significant interaction between litter type and time on N concentration ($F_{4,72}=4.39$, $p<0.05$). All litter types showed an increase in N concentration over time, although the extent of the increase differed between litter types. Thus, N concentration increased steadily for *R. taedigera* and *C. panamensis*, whereas the values for *Cyperus* sp. were similar at Weeks 0 and 1 but more than doubled between Weeks 1 to 12. By week 1, N concentration in litter from *C.*

panamensis had increased to levels similar to those for *R. taedigera* and *Cyperus* sp., which remained similar to the values at Week 0. By week 12, N concentrations for *Cyperus* sp. were almost double those for *R. taedigera* and *C. panamensis*. There were no other significant interaction effects ($p>0.05$).

The water-extractable P fraction was significantly affected by litter type, time and WT treatments (Fig. 7.3e, f; Table 7.1). Mean extractable P concentration was greatest in *R. taedigera* litter, followed by *C. panamensis* and finally *Cyperus* sp. Extractable P concentrations dropped sharply initially before remaining the same. The low WT treatment increased the quantity of water-extractable P for all litter types. There was a significant WT treatment x time interaction ($F_{1,57}=13.95$, $p<0.001$) because extractable P increased significantly in the high WT treatment between Weeks 1 to 12, while the opposite occurred in the low WT treatment. Litter type, time and the WT treatments showed significant interactions with regard to P concentrations.

The C:N ratio for the water extractable fraction differed significantly between litter types as the values for *R. taedigera* and *C. panamensis* litter were similar and almost double that for *Cyperus* sp. There was a significant effect of time as C:N ratio decreased more than 4-fold between Weeks 0 and 1, and this was followed by a small decrease between Weeks 1 and 12. At Week 0, C:N ratios differed significantly between litter types, being greatest for *C. panamensis* and smallest for *Cyperus* sp. However, C:N ratios within the labile fraction converged with time and were similar for all litter types by Week 12. Water table had a significant effect on C:N ratios as the values were greater in the low WT treatment; the effect of WT became more pronounced with time (Fig. 7.4a, b; Table 7.2). The C:N ratio for *Cyperus* sp. litter remained similar in

both WT treatments over time, whereas the values for *R. taedigera* and *Cyperus* sp. litter had decreased significantly by Week 12.

The C:P ratios were greatest for *Cyperus* sp. litter and smallest for *R. taedigera* (Fig 7.4c, d; Table 7.2). Significant interaction effects between litter type, time and WT treatment were apparent, although the ratios were similar across all litter types and WT treatments except for the high WT treatment of *Cyperus* sp. which showed a significant increase between Weeks 1 and 12.

N:P ratios were significantly affected by litter type, the values for *Cyperus* sp. litter being 6-fold greater than those for *C. panamensis* and 16-fold greater than for *R. taedigera* (Fig 7.4e, f; Table 7.2). The significant litter type x time interaction highlights the significant increase in the C:P ratio for *Cyperus* sp. litter between Weeks 0 and 12, whereas the values for *R. taedigera* and *C. panamensis* did not vary significantly with time and were lower than for *Cyperus* sp. at Week 12.

7.3.2.2.2 Acid extractable C, N and P

Acid extractable C concentrations were significantly affected by litter type, time and WT (Fig. 7.5a, b; Table 7.3) All mean C concentrations decreased with time and a significant effect of site x time interactions was found ($F_{4,71}=5.90$, $p<0.001$).

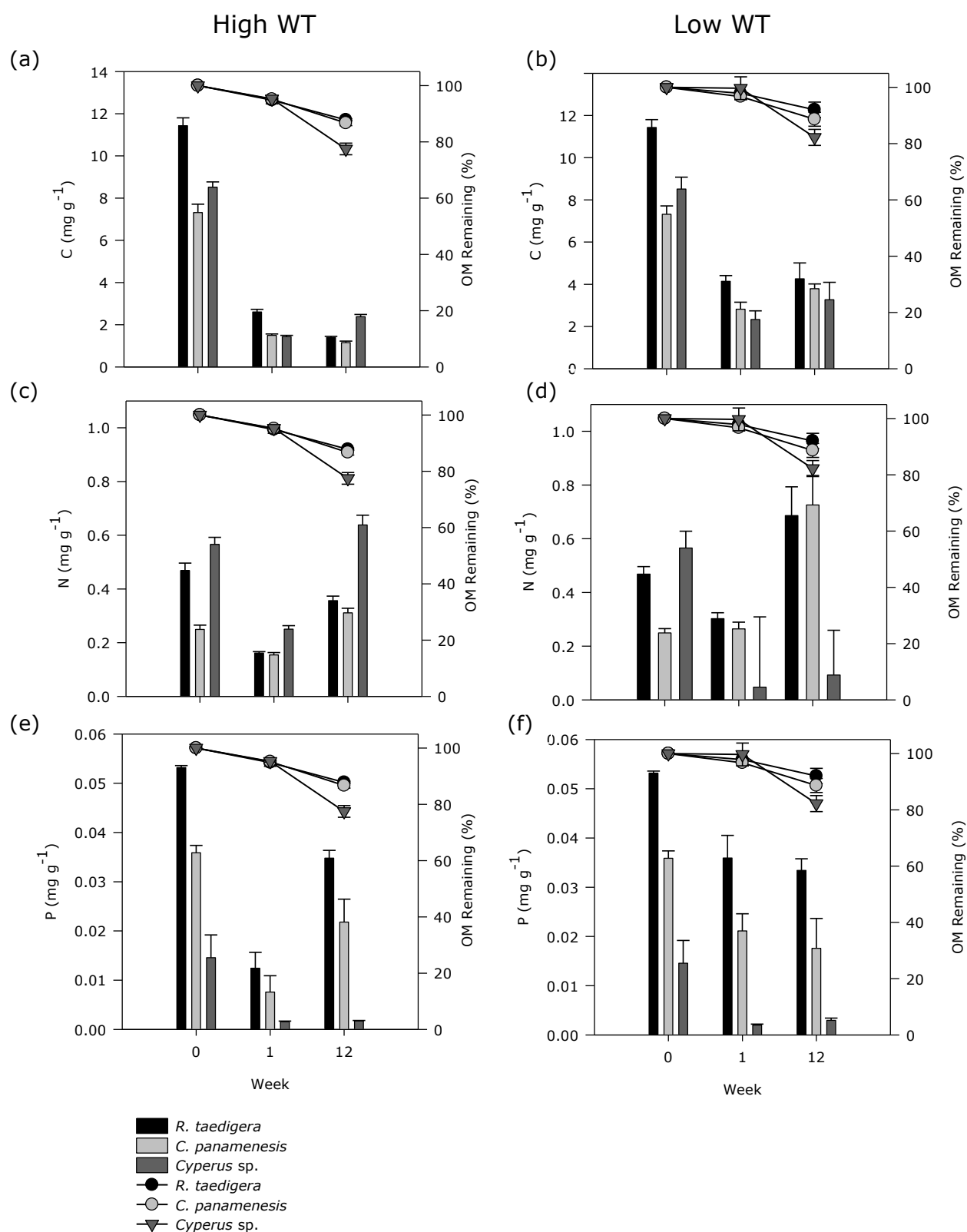


Figure 7.3. Water extractable carbon (a, b), nitrogen (c, d) and phosphorus (e, f) at three time points in the high WT (a, c, e) and low WT treatments (b, d, f histograms). Single standard errors of the mean (n=5) are shown. Organic matter remaining (% , line diagrams) is shown on the right hand Y-axis.

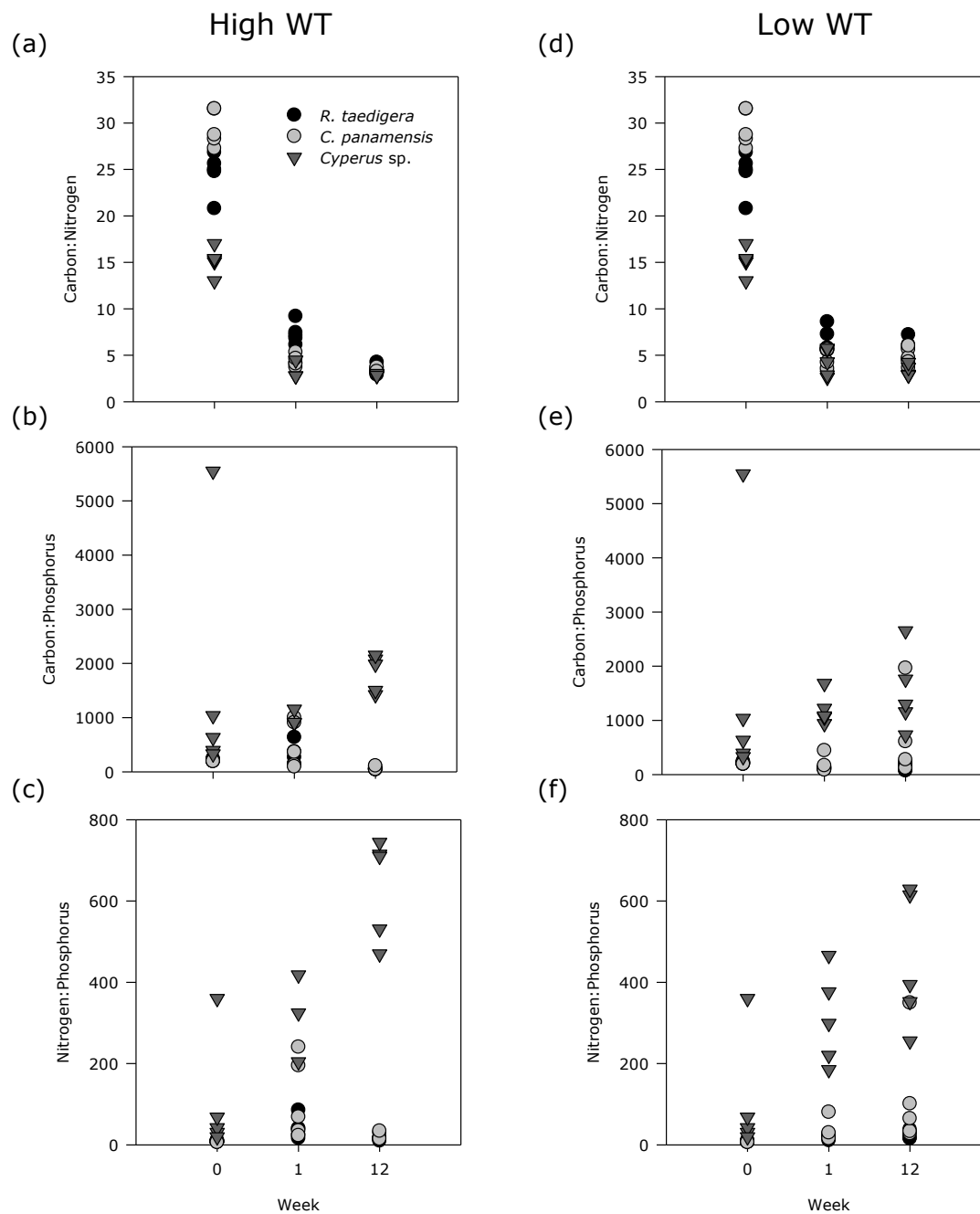


Figure 7.4. Water extractable ratios in weeks 0, 1 and 12 for litter from *R. taedigera*, *C. panamensis* and *Cyperus sp.* in the High WT (a-c) and Low WT treatments (d-f).

Table 7.1. *F* and *p* values from ANOVA for water extractable carbon, nitrogen and phosphorus with 'litter type', 'time' and 'WT' as factors. Significant values are indicated in bold.

	Litter type	Carbon Time	WT	Litter type	Nitrogen Time	WT	Litter type	Phosphorus Time	WT
<i>F</i>	9.47	166.34	93.31	17.16	25.35	52.35	71.84	29.88	8.77
<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.05

Table 7.2. *F* and *p* values from ANOVA for water extractable carbon:nitrogen, carbon:phosphorus and nitrogen:phosphorus ratios with 'litter type', 'time' and 'WT' as factors. Significant values are indicated in bold.

	Carbon:Nitrogen			Carbon:Phosphorus			Nitrogen:Phosphorus		
	Litter type	Time	WT	Litter type	Time	WT	Litter type	Time	WT
<i>F</i>	67.12	1260.85	11.31	27.63	0.40	0.00	97.67	16.38	1.81
<i>p</i>	<0.001	<0.001	<0.05	<0.001	0.7	0.9	<0.001	<0.001	0.2

Mean C concentrations found in the *Cyperus* sp. litter were greatest throughout, with an initial C concentration of 125 mg g⁻¹ and a final concentration of 100 mg g⁻¹ under both water table treatments. *R. taedigera* mean initial C concentration was 99 mg g⁻¹ which decreased to 89 mg g⁻¹ under the high WT and 87 mg g⁻¹ under the low WT. *C. panamensis* had the lowest acid extractable C with an initial concentration of 76 mg g⁻¹ decreasing to 61 mg g⁻¹ under the low WT and 57 mg g⁻¹ under the high WT.

Acid extractable N concentrations were significantly affected by litter type. No significant time effects were found, though all litter types decreased in N concentration relative to the initial N concentrations. A near significant interaction effect of time x WT was seen ($F_{1,56}=3.62$, $p=0.064$). Initial N concentrations were greatest in the *R. taedigera* litter at 7.4 mg g⁻¹ which decreased to between 4.9 - 5.2 mg g⁻¹ in weeks 1 and 12 under the high WT and to 6.2 mg g⁻¹ at week 1 under the low WT, further decreasing to a concentration of 4.6 mg g⁻¹ in week 12. *C. panamensis* litter N concentrations were 5.4 mg g⁻¹ initially which then decreased to 4.5 mg g⁻¹ in week 12 under the low WT and 4.2 mg g⁻¹ under the high WT.

Acid extractable P was found for all three sites in the initial litter only (Fig. 7.5 e, f) and was significantly affected by litter type and time. P was only extracted in weeks 1 and 12 from the *R. taedigera* litter, with concentrations near to zero (0.00088 mg g⁻¹ week 1 and 0.00003 mg g⁻¹ week 12). *R. taedigera* had the greatest initial P concentration with 0.080 mg g⁻¹, followed by *C. panamensis* with an average P concentration of 0.054 and the lowest from the *Cyperus* sp. litter with 0.022 mg g⁻¹.

The C:N ratios for the acid extractable fraction were significantly affected by litter type only (Fig. 7.6a, b; Table 7.4). Similar ratios were found for the *R. taedigera* and *C. panamensis* litter (range 9 - 18) and were lower than those found from the *Cyperus* sp. litter (26 - 66). This was true for weeks 1 and 12 also, though ratios increased in magnitude weeks 0 - 1 and decreased from weeks 1 - 12 under the high WT, the opposite was seen under the low WT treatment.

C:P ratios were significantly affected by litter type and time (Fig. 7.6c, d; Table 7.4). Initial C:P ratios (week 0) were the greatest in the *Cyperus* sp. litter (range 3141 - 64704)) and were lower and similar from the *R. taedigera* and *C. panamensis* litters (range 1158 - 1634). All ratios decreased to zero at week 1 and were significantly greater in week 12 (range 324333 - 1002084). This was similar for both high and low WTs.

N:P ratios were significantly affected by litter type and time, with substantial increases in ratios from weeks 0 - 12 under both WT treatments. Initial ratios were greatest in the *Cyperus* sp. litter (range 114 - 2460) and lower and similar for the *R. taedigera* (range 66 - 107) and *C. panamensis* (range 86 - 112) litters. All ratios increases from weeks 0 - 12 with the *C. panamensis* found to have the greatest ratios under both WT treatments in the range 32064 - 84208. *R. taedigera* litter ratios at week 12 were 20672 - 23113 and *Cyperus* sp. litter ratios were 15079 - 25940.

7.3.2.2.3 Recalcitrant C, N and P content

The non-acid-extractable residue contained the highest concentrations of C and N, whereas the P concentration was an order of magnitude lower than in the water and acid extractable fractions. Recalcitrant C held in the residual component of the litter

was significantly affected by litter type, time and WT treatment (Fig. 7.7a, b; Table 7.5). The interaction between time and WT treatment was also significant ($F_{1,57}=11.90$, $p<0.05$). The concentrations of recalcitrant C were similar for *R. taedigera* and *Cyperus* sp. litter, although the values were significantly lower than in the litter of *C. panamensis*. The concentration of C in the residue was greatest at Week 1, while the values for Weeks 0 and 12 were similar. Recalcitrant C concentrations were higher in the high WT treatment. The concentration of recalcitrant N was significantly affected by time (Fig. 7.7c, d; Table 7.5) as the highest values were observed in Week 1, whereas the concentrations recorded at Weeks 0 and 12 were lower and similar in magnitude.

The recalcitrant N concentrations for *R. taedigera* and *C. panamensis* were similar in both WT treatments, whereas the corresponding values for *Cyperus* sp. were greatest under the high WT (Fig. 7.7c, d; Table 7.5). *C. panamensis* had significantly higher residual N concentration in the low WT treatment than *Cyperus* sp.

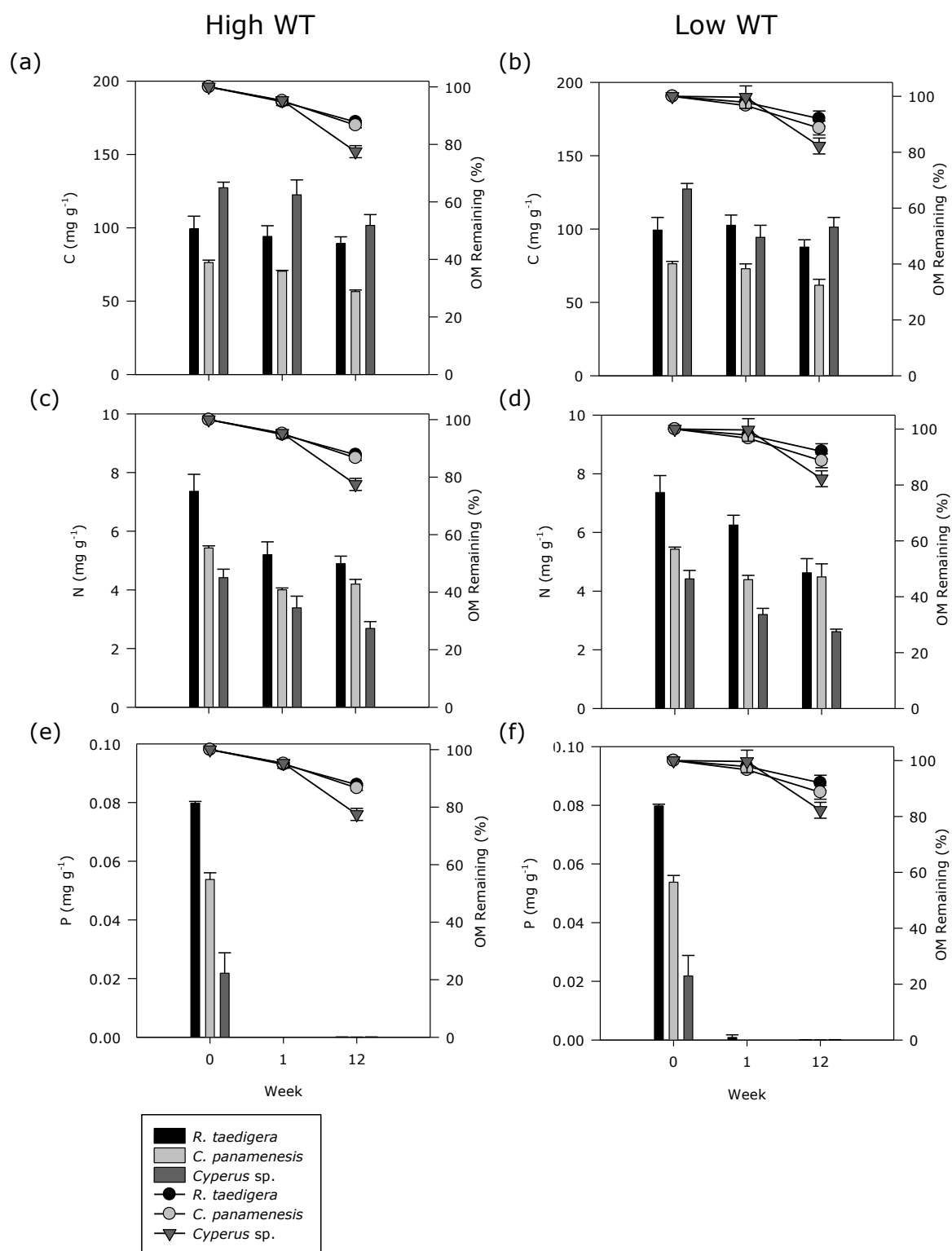


Figure 7.5. Acid extractable carbon (a, b), nitrogen (c, d) and phosphorus (e, f) at three time points in the high WT (a, c, e) and low WT treatments (b, d, f histograms). Single standard errors of the mean (n=5) are shown. Organic matter remaining (% , line diagrams) is shown on the right hand Y-axis.

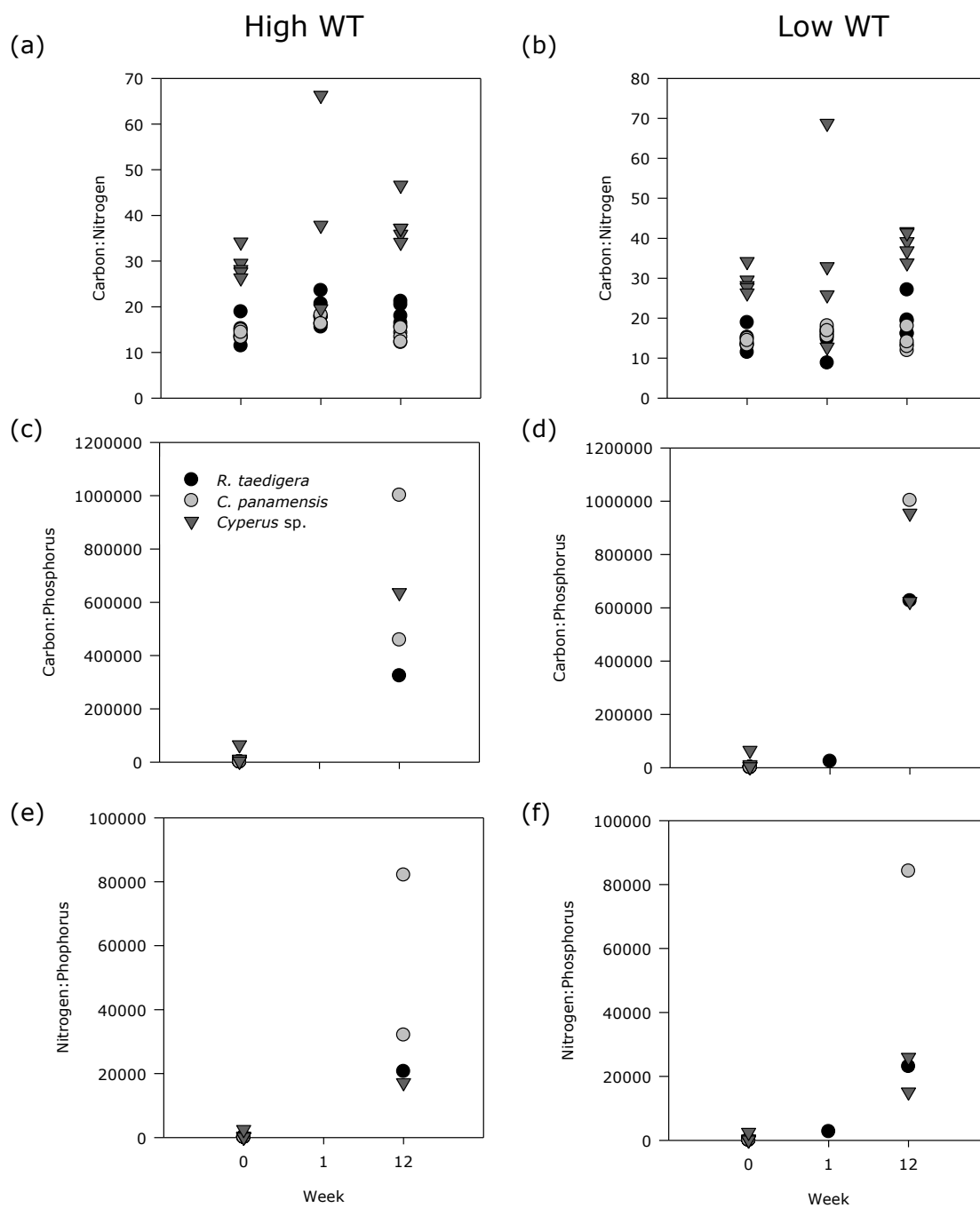


Figure 7.6. Acid extractable ratios in weeks 0, 1 and 12 for litter from *R. taedigera*, *C. panamensis* and *Cyperus sp.* in the High WT (a-c) and Low WT treatments (b-e).

Table 7.3. Acid extractable Carbon, Nitrogen and Phosphorus, ANOVA *F* and *p* values with factors 'litter type', 'time' and 'WT'. Significant values are indicated in bold. Near significant results in italics.

	Litter type	Carbon Time	WT	Litter type	Nitrogen Time	WT	Litter type	Phosphorus Time	WT
<i>F</i>	111.21	7.70	4.51	24.59	1.46	0.22	50.44	934.65	0.88
<i>P</i>	<0.001	0.001	<0.05	<0.001	0.2	0.6	<0.001	<0.001	0.4

Table 7.4. Acid extractable Carbon:Nitrogen, Carbon:Phosphorus and Nitrogen:Phosphorus ratios, ANOVA *F* and *p* values with factors 'litter type', 'time' and 'WT'. Significant values are indicated in bold. Near significant results in italics.

	Carbon:Nitrogen			Carbon:Phosphorus			Nitrogen:Phosphorus		
	Litter type	Time	WT	Litter type	Time	WT	Litter type	Time	WT
<i>F</i>	62.12	2.21	0.45	18.71	152.29	8.67	71.54	70.27	2.73
<i>p</i>	<0.001	0.1	0.5	<0.001	<0.001	0.1	<0.001	<0.001	0.2

Recalcitrant P concentrations were significantly affected by litter type, time and the interaction between these variables (Fig. 7.7e, f; Table 7.5; Interaction: $F_{4,71}=4.78$, $p<0.05$). The values were highest for *Cyperus* sp. followed by *R. taedigera*; residual P concentration was almost zero in *C. panamensis*. The values were similar at Weeks 0 and 12, when residual P concentrations were significantly greater than at Week 1. Residual P concentrations were undetectable in *C. panamensis* litter at all sampling dates, while the values for *R. taedigera* were significantly greater than those for *Cyperus* sp in Weeks 0 and 12.

C:N ratios for the residual fraction showed no significant variation over time or between litter types and WT treatments (Fig. 7.8a, d; Table 7.6).

By contrast, C:P ratios differed significantly between litter types and over time and there was a significant interaction between these factors (Fig. 7.8a, d; Table 7.6; Interaction: $F_{4,55}=21.13$, $p<0.001$). The C:P ratio was greatest for *C. panamensis*, followed by *R. taedigera* and finally *Cyperus* sp.

N:P ratios for the residual fraction varied significantly with time and between litter types (Fig. 7.8c, f; Table 7.6). Generally the smallest ratios were found from *Cyperus* sp. litter. Ratios for *C. panamensis* litter were much greater in week 12 than the corresponding values for *R. taedigera* and *Cyperus* sp.

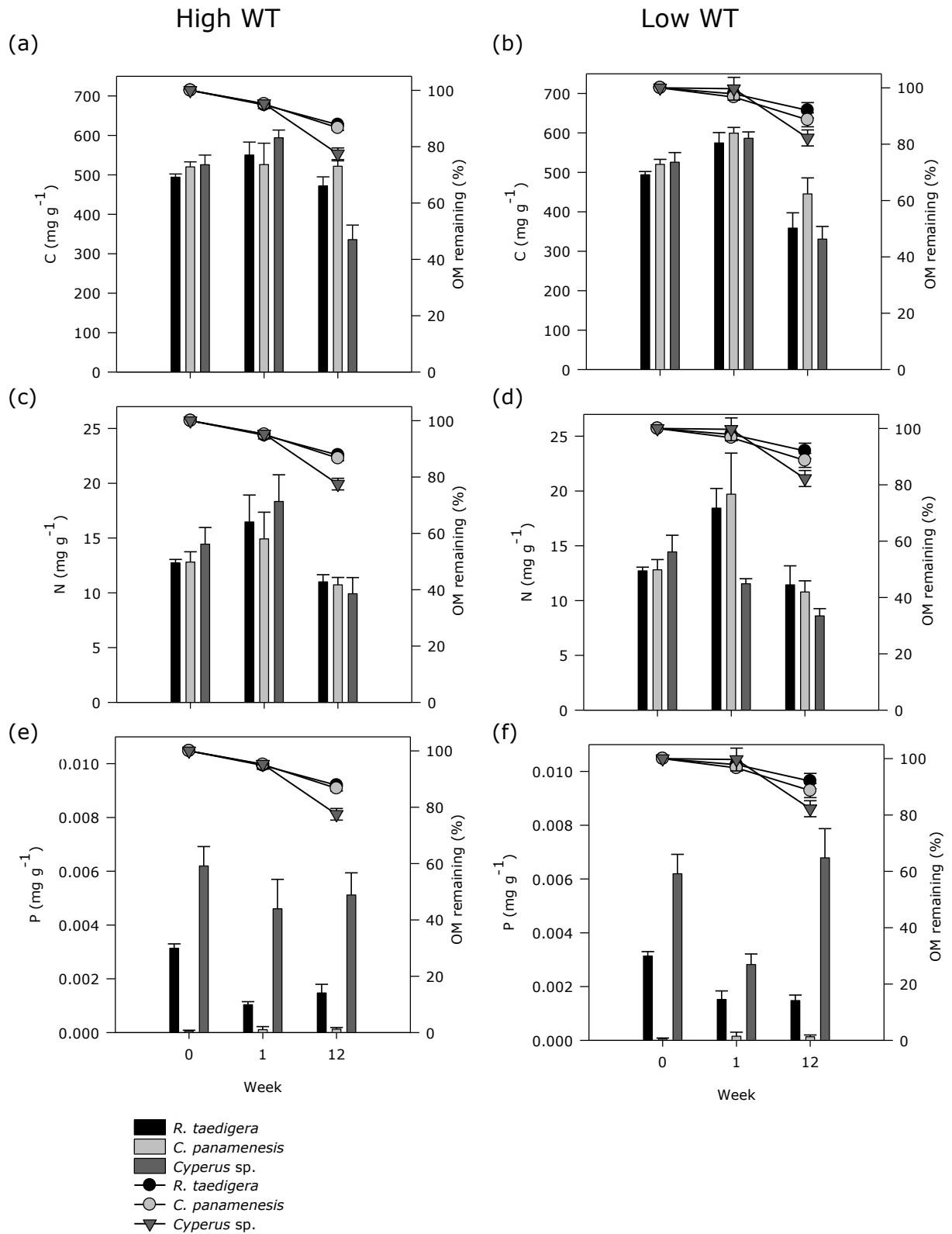


Figure 7.7. Residual carbon (a, b), nitrogen (c, d) and phosphorus concentrations (e, f) at three times points in the high WT (a, c, e,) and low WT treatments (b, d, f, histograms). Single standard errors of the mean (n=5) are shown. Organic matter remaining (% , line diagrams) is shown on the right hand Y-axis.

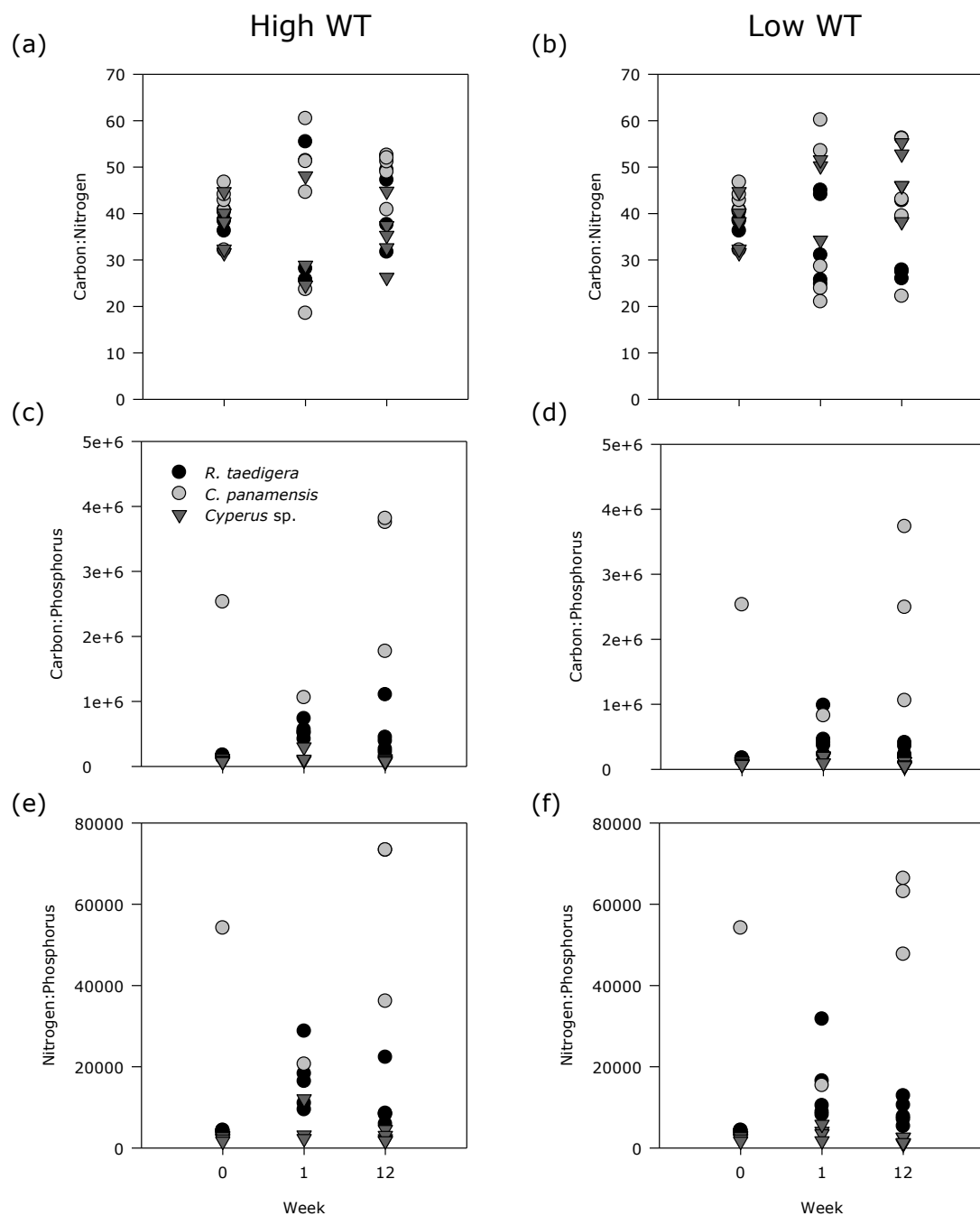


Figure 7.8. C:N (a, b), C:P (c, d) and N:P (e, f) ratios in the residual fraction in weeks 0, 1 and 12 for *R. taedigera*, *C. panamensis* and *Cyperus sp.* litter in the High WT (a,c,e) and (b,d,f) Low WT treatments.

Table 7.5. *F* and *p* values from ANOVA for residual carbon, nitrogen and phosphorus with 'litter type', 'time' and 'WT' as factors. Significant values are indicated in bold and near-significant results are shown in italics.

	Carbon			Nitrogen			Phosphorus		
	Litter type	Time	WT	Litter type	Time	WT	Litter type	Time	WT
<i>F</i>	2.70	8.00	5.66	0.24	7.42	1.18	120.30	6.15	0.20
<i>P</i>	0.075	<0.001	<0.05	0.8	<0.05	0.3	<0.001	<0.05	0.7

Table 7.6. *F* and *p* values from ANOVA for residual carbon:nitrogen, carbon:phosphorus and nitrogen:phosphorus ratios with 'litter type', 'time' and 'WT' as factors. Significant values are indicated in bold.

	Carbon:Nitrogen			Carbon:Phosphorus			Nitrogen:Phosphorus		
	Litter type	Time	WT	Litter type	Time	WT	Litter type	Time	WT
<i>F</i>	1.27	0.14	0.03	147.98	12.81	2.72	238.35	21.32	1.25
<i>p</i>	0.3	0.9	0.9	<0.001	<0.001	0.1	<0.001	<0.001	0.3

7.3.3 Effect of nutrient amendments on enzyme activity

The activities of all five enzymes examined were significantly affected by the site from which the peat material was sourced. Mean phosphomonoesterase activity was greatest for the *Cyperus* sp. site, followed by the *R. taedigera*, and *C. panamensis* sites (Fig. 7.9a). Phosphodiesterase activity (Fig. 7.9b) was greater for peat from the *Cyperus* sp. site than for the *R. taedigera* and *C. panamensis* sites.

This pattern was repeated for β -xylanase activity, although on a different scale (Fig. 7.9e). B-glucosidase activity was also greatest for the *Cyperus* sp. site, followed successively by the *C. panamensis* and *R. taedigera* sites (Fig. 7.9c). The only enzyme which did not show the greatest mean activity for peat from the *Cyperus* sp. was cellobiohydrolase, which was for the *R. taedigera* site, followed by the *Cyperus* sp. and *C. panamensis* sites (Fig. 7.9d).

The nutrient treatments imposed had no significant effect on enzyme activity for any of the sites examined although the tendency for phospho-monoesterase activity to be greater in the higher N amendment treatments approached significance at the *R. taedigera* site (Figs. 7.10- 7.12).

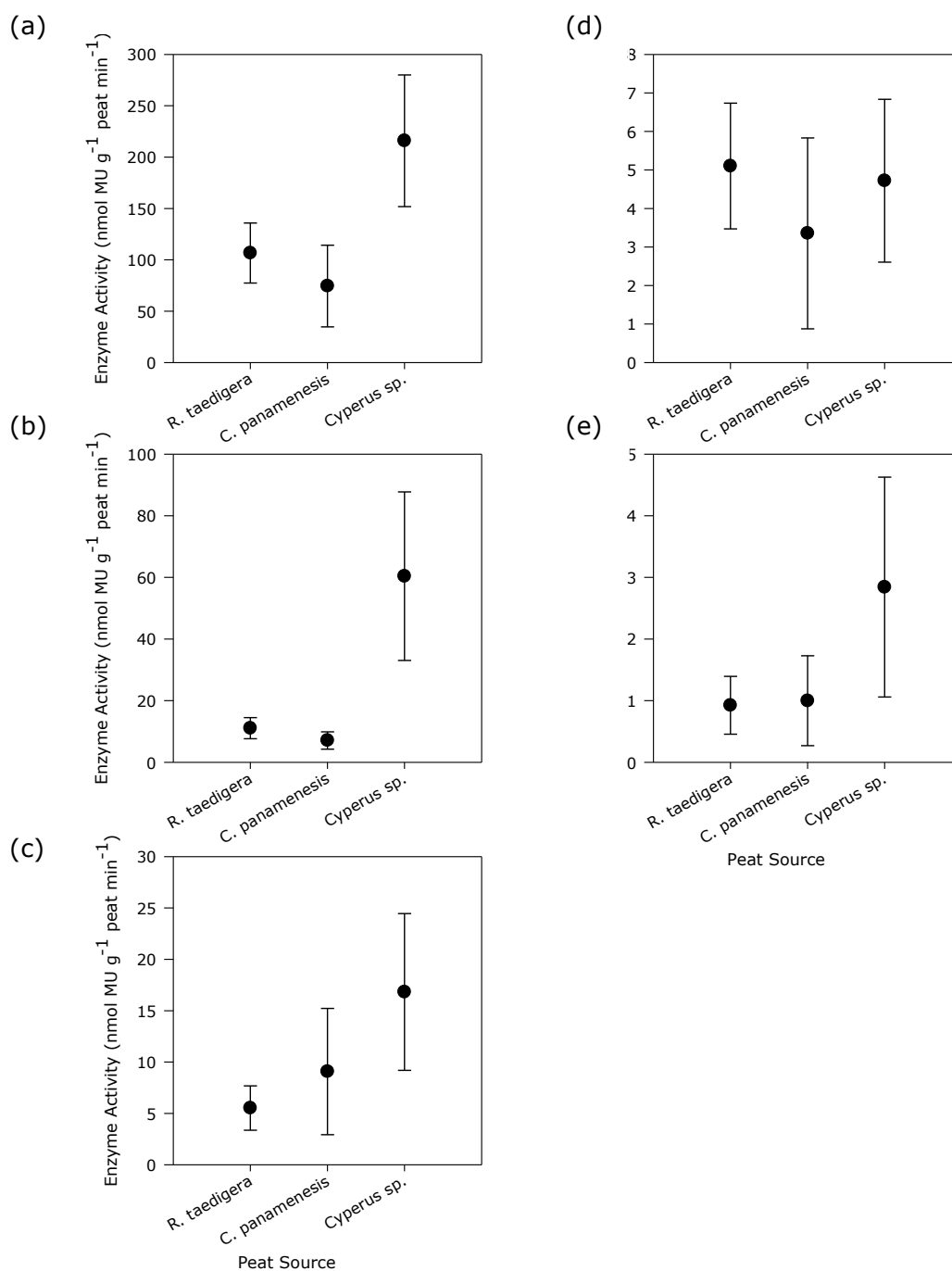


Figure 7.9. Mean enzyme activities for all three peat sources including all nutrient amendments and bases with the addition of different substrates: a) phosphomonoesterase, b) phosphodiesterase, c) β-glucosidase, d) cellobiohydrolase and e) β-xylanase. The standard deviation is shown. Summary of ANOVA analysis:

(a)	Site:	$F_{2,62} = 47.80, p < 0.001$
(b)	Site:	$F_{2,62} = 19.50, p < 0.001$
(c)	Site:	$F_{2,62} = 74.99, p < 0.001$
(d)	Site:	$F_{2,62} = 3.57, p = 0.037$
(e)	Site:	$F_{2,62} = 16.92, p < 0.001$

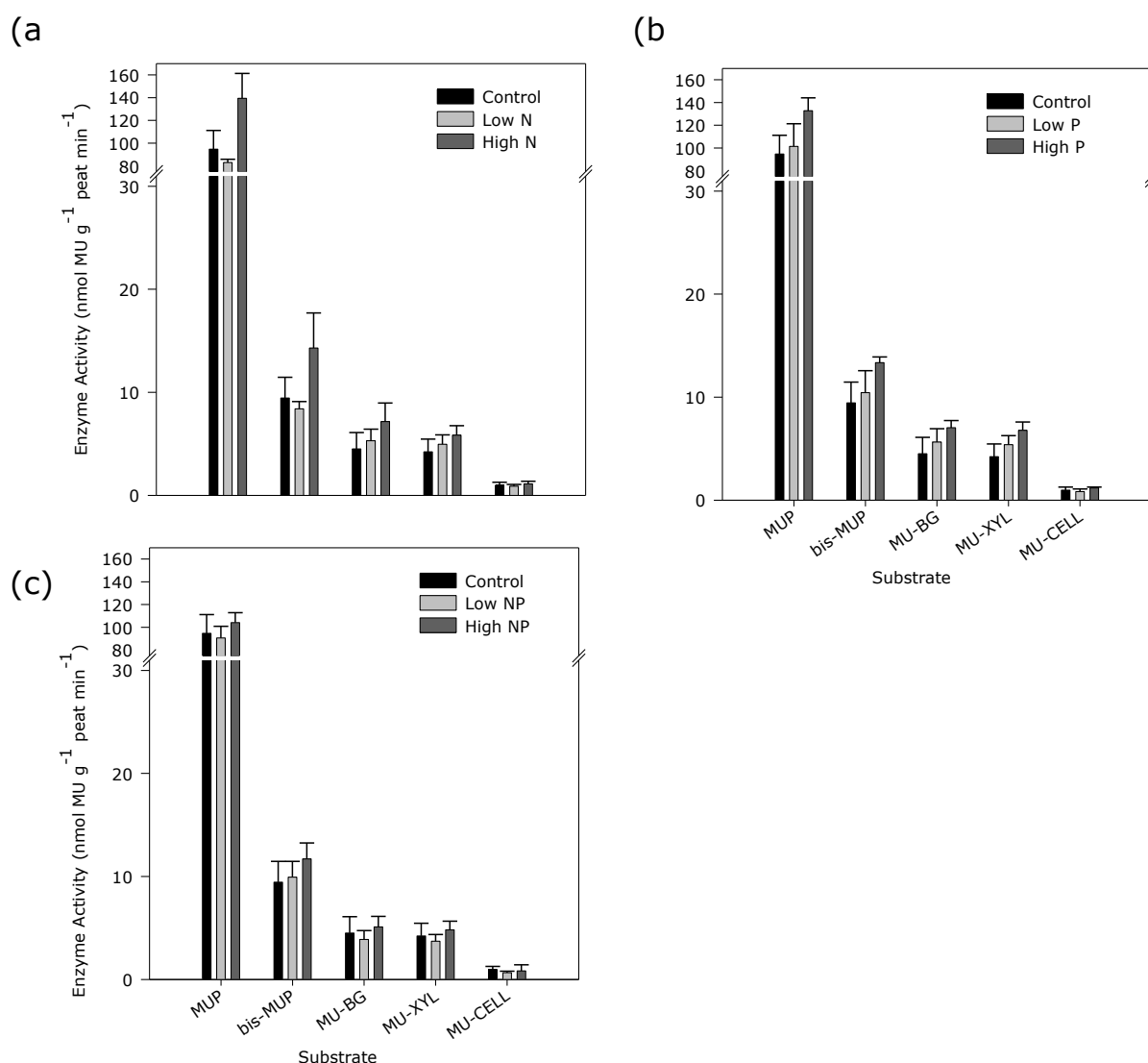


Figure 7.10. Activities of five enzymes in the control and low and high P, N and N + P nutrient amendment treatments for peat from the *R. taedigera* site for: a) N; b) P and c) N+P. Single standard errors of the mean are shown (n=3). ANOVA summaries:

- a) MUP: $F_{2,8} = 3.50$, $p = 0.07$.
 bis-MUP: $F_{2,8} = 1.84$, $p = 0.2$.
 MU-BG: $F_{2,8} = 0.79$, $p = 0.5$.
 MU-XYL: $F_{2,8} = 0.61$, $p = 0.6$.
 MU-CELL: $F_{2,8} = 0.21$, $p = 0.8$.
- b) MUP: $F_{2,8} = 1.56$, $p = 0.3$.
 bis-MUP: $F_{2,8} = 1.39$, $p = 0.3$.
 MU-BG: $F_{2,8} = 1.01$, $p = 0.4$.
 MU-XYL: $F_{2,8} = 1.69$, $p = 0.3$.
 MU-CELL: $F_{2,8} = 0.63$, $p = 0.6$.
- c) MUP: $F_{2,8} = 0.32$, $p = 0.7$.
 bis-MUP: $F_{2,8} = 0.48$, $p = 0.6$.
 MU-BG: $F_{2,8} = 0.26$, $p = 0.8$.
 MU-XYL: $F_{2,8} = 0.35$, $p = 0.7$.
 MU-CELL: $F_{2,8} = 0.17$, $p = 0.8$.

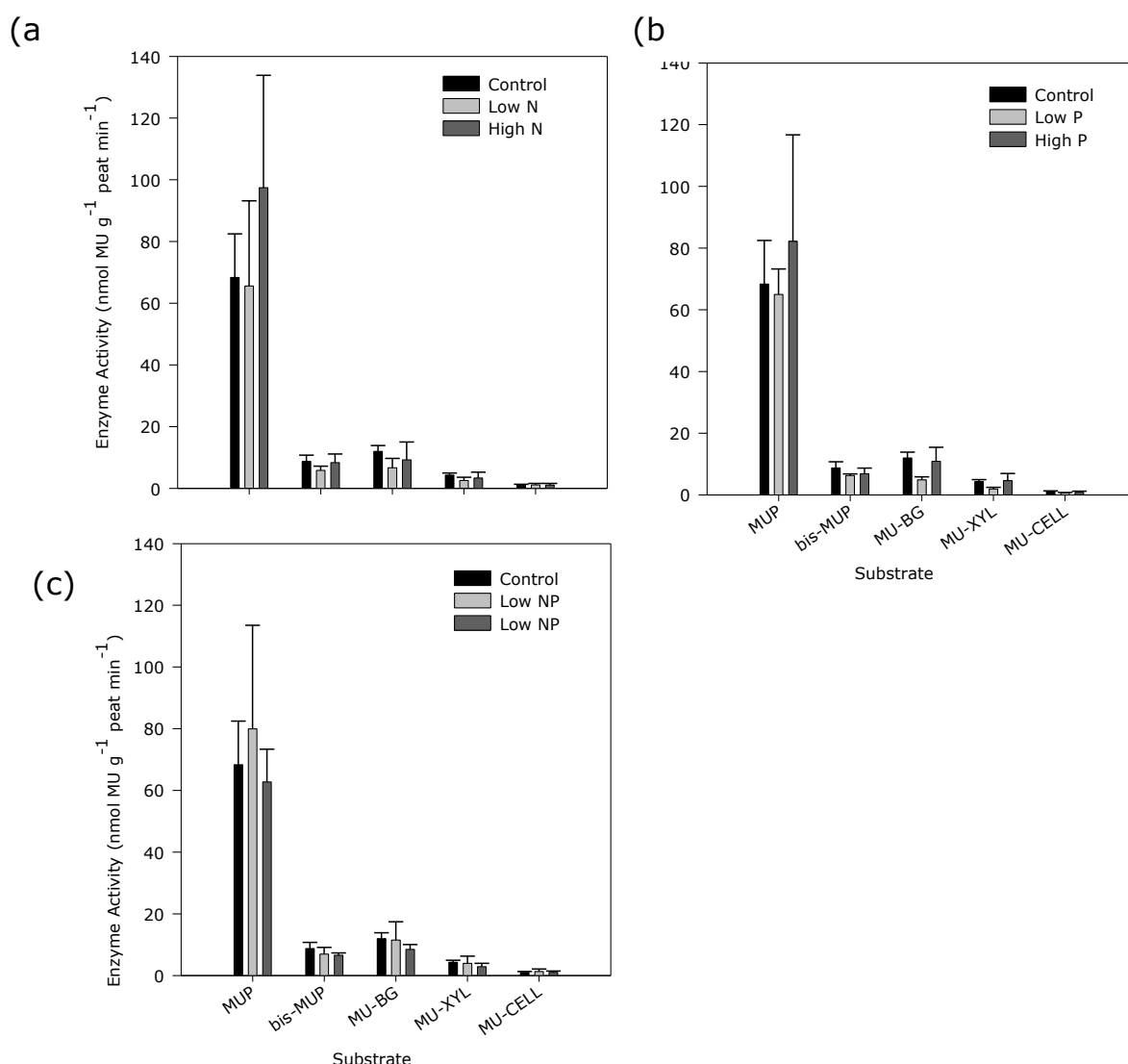


Figure 7.11. Activities of five enzymes in the control and low and high P, N and N + P nutrient amendment treatments for peat from the *C. panamensis* site for: a) N; b) P and c) N+P. Single positive standard errors of the mean are shown (n=3). ANOVA summaries:

- a) MUP: $F_{2,8} = 0.41$, $p = 0.7$.
 bis-MUP: $F_{2,8} = 0.57$, $p = 0.6$.
 MU-BG: $F_{2,8} = 0.46$, $p = 0.7$.
 MU-XYL: $F_{2,8} = 0.46$, $p = 0.7$.
 MU-CELL: $F_{2,8} = 0.01$, $p = 1$.
- b) MUP: $F_{2,8} = 0.17$, $p = 0.8$.
 bis-MUP: $F_{2,8} = 0.65$, $p = 0.6$.
 MU-BG: $F_{2,8} = 1.75$, $p = 0.3$.
 MU-XYL: $F_{2,8} = 1.10$, $p = 0.4$.
 MU-CELL: $F_{2,8} = 0.59$, $p = 0.6$.
- c) MUP: $F_{2,8} = 0.16$, $p = 0.9$.
 bis-MUP: $F_{2,8} = 0.45$, $p = 0.7$.
 MU-BG: $F_{2,8} = 0.27$, $p = 0.8$.
 MU-XYL: $F_{2,8} = 0.24$, $p = 0.8$.
 MU-CELL: $F_{2,8} = 0.08$, $p = 0.9$.

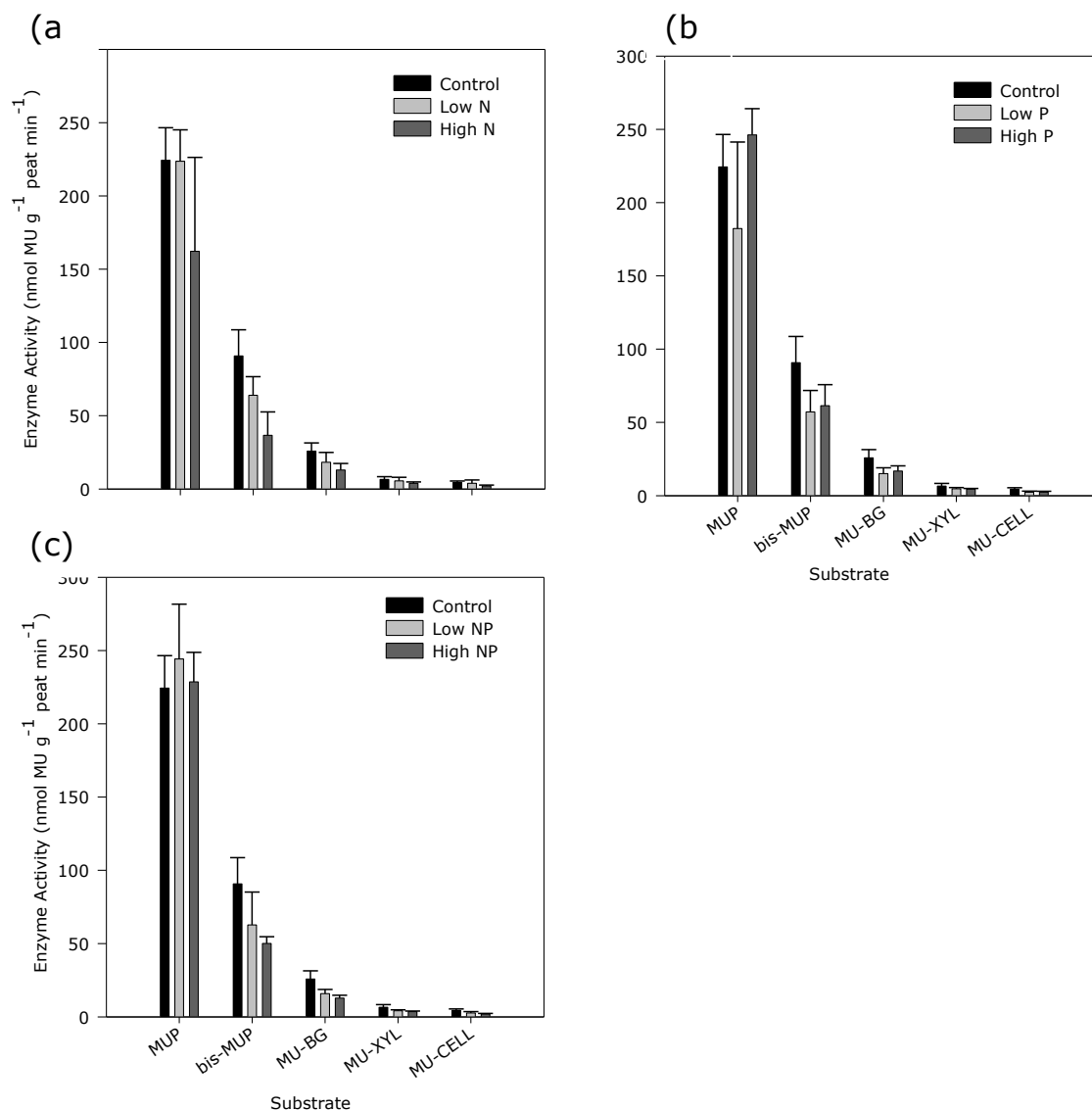


Figure 7.12. Activities of five enzymes in the control and low and high P, N and N + P nutrient amendment treatments for peat from the *Cyperus* sp. site for: a) N; b) P and c) N+P. Single standard errors of the mean are shown (n=3). ANOVA summaries:

- a) MUP: $F_{2,8} = 0.75$, $p = 0.5$.
bis-MUP: $F_{2,8} = 2.99$, $p = 0.1$.
MU-BG: $F_{2,8} = 1.32$, $p = 0.3$.
MU-XYL: $F_{2,8} = 0.56$, $p = 0.6$.
MU-CELL: $F_{2,8} = 0.69$, $p = 0.5$.
- b) MUP: $F_{2,8} = 0.74$, $p = 0.5$.
bis-MUP: $F_{2,8} = 1.36$, $p = 0.3$.
MU-BG: $F_{2,8} = 1.70$, $p = 0.3$.
MU-XYL: $F_{2,8} = 0.95$, $p = 0.4$.
MU-CELL: $F_{2,8} = 2.10$, $p = 0.2$.
- c) MUP: $F_{2,8} = 0.14$, $p = 0.9$.
bis-MUP: $F_{2,8} = 1.54$, $p = 0.3$.
MU-BG: $F_{2,8} = 3.24$, $p = 0.1$.
MU-XYL: $F_{2,8} = 1.97$, $p = 0.2$.
MU-CELL: $F_{2,8} = 2.37$, $p = 0.2$.

7.4 Discussion

7.4.1 Organic matter mass loss rates in three litter types.

The most rapid mass loss of organic matter (OM) was seen in the *C. panamensis* litter (Fig. 7.1b, e), which would usually suggest that there is a high proportion of labile material relative to recalcitrant material, as labile material is rapidly leached after deposition of litter (Yule and Gomez, 2009). However, comparison of the chemical characteristics of the litter reveals that the litter from *R. taedigera* and *C. panamensis* contained similar quantities of labile and semi-labile C and nutrients (Fig. 7.2), yet *R. taedigera* litter did not exhibit the same rapid initial loss of OM (Fig. 7.1a, b). The initial decomposition rate of litter from *Cyperus* sp. was comparable to that of *R. taedigera* (Fig. 7.1b, f) and a greater overall percentage of OM was lost (Fig. 7.1 a, e). The greater OM mass loss from *Cyperus* sp. litter is unexpected as its labile and semi-labile P concentrations were low (Fig. 7.2). This, in combination with the relatively high C:P and N:P ratios, would usually suggest low rates of decomposition (Bragazza *et al.*, 2006; Wang *et al.*, 2010), particularly compared to the other two litter types. The high phosphatase activity at this site relative to the *R. taedigera* and *C. panamensis* sites indicates that P is limiting and would suggest a decreased decomposition rate. This is supported by the virtually zero P concentrations found from the acid extractable fraction of the litter (representing semi-labile fractions; Fig. 7.5 e, f). The measured enzyme activities also suggest that the *C. panamensis* site was the least limited by nutrient availability as activities were lowest at this site (Olander and Vitousek, 2000; Fig. 7.11), although activities at the *R. taedigera* site were similar (Fig. 7.10). The peat at the *R. taedigera* and *C. panamensis* sites is known to contain higher total and dissolved amounts of C and nutrients (*cf.* Section 4.3.2). Overall, the concentrations of labile and semi-labile C and nutrients within the three litter types suggest that the decomposition rate should be greatest at the *R. taedigera* site, followed by the *C. panamensis* and finally by the *Cyperus* sp. sites. However, except for the high initial rate of OM loss in

C. panamensis, this was not seen, demonstrating that factors other than labile C and nutrient concentrations in the litter were responsible for determining decomposition rate, for example the composition of the microbial communities (Allison *et al.*, 2007).

7.4.2 Influence of water table on loss of litter mass

The litter types differed in their patterns of mass loss over time, probably due to differences in substrate quality. *R. taedigera* (Fig. 7.1a) showed a smaller and more gradual loss of litter mass in both WT treatments (17.4 and 18.2 %) than *C. panamensis* and *Cyperus* sp., although the difference between WT treatments was not significant. The slow decomposition rate of *R. taedigera* litter suggests that it contained a greater proportion of recalcitrant material and little labile material as the latter breaks down rapidly at the start of the decomposition process (Updegraff *et al.*, 1995); the slow loss of biomass also suggests that lignin content was high and cellulose content was low in litter from *R. taedigera* as lignin is recalcitrant and slow to degrade (Jonasson *et al.*, 1999).

C. panamensis (Fig. 7.1b) exhibited the greatest initial mass loss of all litter types (28.7 vs. 38.6 % respectively in the high and low WT treatments); thereafter, the initially high rate of decomposition decreased to $<0.02\% \text{ d}^{-1}$ between sampling events. The initially high mass loss suggests that *C. panamensis* provided the highest quality litter of the three types examined as the high initial loss suggests a relatively high pool of soluble organic material (Updegraff *et al.*, 1995; Jonasson *et al.*, 1999; Yule and Gomez, 2009).

Cyperus sp. (Fig. 7.1c) was the only species to provide litter in which decomposition was initially slow but subsequently increased with time. As *Cyperus* sp. produces litter with a high cellulose to lignin ratio (Debusk *et al.*, 2005), the slow initial rate of decomposition was unexpected, but might be linked to the low concentrations of labile P in this litter type.

Several studies suggest that the initial rate of litter decomposition is determined by the composition of the litter itself rather than nutrient availability in the system; thus, although soils may be nutrient-poor, the litter will not necessarily be decomposed rapidly to provide nutrients (Aerts *et al.*, 2003; Debusk *et al.*, 2005; Yule and Gomez, 2009). This conclusion is reflected by the present study as the hypothesis that litter from the most nutrient-poor site would decompose most rapidly proved false; in reality, litter from the site regarded as being intermediate in its nutrient status (*C. panamensis*) exhibited the greatest initial and overall mass losses. The three litter types also showed different patterns of nutrient release, with litter from the nutrient-rich and nutrient-poor sites (*R. taedigera* and *Cyperus* sp. respectively) demonstrating a slower and more gradual release of nutrients rather than the brief pulse seen when decomposition began in litter from *C. panamensis*.

Overall, the hypothesis that litter exposed to the low WT treatment would experience a greater mass loss proved true for two of the three litter types examined as *C. panamensis* and *Cyperus* sp. exhibited significant differences between WT treatments, whereas *R. taedigera* showed no significant effect. It would be anticipated that litter would decompose more rapidly in the low WT treatment due to the predominance of aerobic decomposition over the slower anaerobic decomposition which would be expected under the high WT conditions (Debusk *et al.*, 2005). Various studies to examine the affects of WT on decomposition processes have produced mixed results. Some, such as that by Padial and Thomaz (2006), found that, contrary to expectations, litter decomposition was greatest under permanently flooded conditions. Moore *et al.* (2007) found that neither dry nor permanently flooded conditions produced the greatest litter mass loss, but instead periodically flooded sites displayed much greater losses. This observation was supported by Makiranta *et al.* (2009), who suggested that neither wet nor dry conditions are optimal for decomposition but that intermediate conditions are most favourable. This view was supported by Battle and Golladay (2007) who suggested that saturated, rather than dry or flooded conditions provide the most favourable decomposition conditions. However other research, including

the present study, indicates that the rates of decomposition processes are increased under low (but still moist) WT conditions (e.g. Szumigalski and Bayley, 1996; Haraguchi *et al.*, 2003; Williams and Yavitt, 2003).

7.4.3 Effect of nutrient amendments on enzyme activity

The patterns of enzyme activity (Figs. 7.10-7.12) provide an insight into the microbial communities within the three peat types examined. For all five enzymes except cellobiohydrolase, activity was greater for peat from the *Cyperus* sp. site. The much greater activity of phosphomonoesterase and phosphodiesterase compared to the *R. taedigera* and *C. panamensis* sites provides an indication of the degree of P limitation in peat from the *Cyperus* sp. site as the high enzyme activity indicates that demand cannot be met by available P within the peat. The activities of P enzymes were generally slightly greater for litter from the *R. taedigera* site compared to the *C. panamensis* site. β -Glucosidase activity increased markedly across the transect, suggesting a greater availability of substrate with increased activity (Sjögersten *et al.*, 2010). However, this would be expected to correspond to increased cellobiohydrolase activity as both enzymes are strongly influenced by substrate availability. The activity of β -Xylanase was low for all three sites, suggesting that the presence of material which degrades slowly was low as the activity of this enzyme is typically linked to material that is slow to decompose (Sjögersten *et al.*, 2010). Enzyme activity in all three peat types was highest for the phosphatases, suggesting the systems were P-limited.

The observation that litter from the *R. taedigera* site exhibited higher enzyme activities following the highest nutrient application for all enzymes and nutrient treatments (Fig. 7.10) suggests that there was still a nutrient limitation to the decomposition process

even when additional nutrients were applied. Of the nutrient treatments applied, the only effect that approached significance was that of the high and low applications of N on phosphomonoesterase activity. This is likely to have resulted from increased demand for P as N availability rose, stimulating the activity of this enzyme to supply additional P to meet demands (Olander and Vitousek, 2000). No other significant effects of nutrient treatments on the activity of individual enzymes were detected, although a significant impact of high and low nutrient application on overall enzyme activity and a significant interaction between nutrient application and enzyme activity were found. The lack of significant individual treatment effects may reflect the limited number of replicates for specific treatments, whereas analysis of the entire database provides sufficient replication to identify the influence of the higher nutrient applications.

Peat from the *C. panamensis* site showed no significant effect of nutrient applications, although enzyme activity tended to be higher following the higher applications of both N and P (Fig. 7.11). The combined high applications of N and P appeared to decrease activity, suggesting that this treatment may have been approaching an excess, possibly inducing an inhibitory effect (Olander and Vitousek, 2000). A similar effect was seen for litter from the *Cyperus* sp. site in the high N and high NP treatments, and this view is supported by the observation that enzyme activity was generally increased above the basal level by the application of supplementary nutrients. It is also possible that these trends are indicative of a response to nutrient applications that might have become increasingly evident with time as greatly increased nutrient supplies would take time to feed through the system to create an inhibitory effect (Olander and Vitousek, 2000). Litter from the *Cyperus* sp. site typically exhibited the greatest enzyme activities,

perhaps because this was the site with the lowest nutrient availability. This effect may have been enhanced because the dense rooting network in the surface peat horizons provided more favourable conditions for microbial populations (Brix, 2007).

Although no significant effects of nutrient application treatments on enzyme activity were detected for any of the peat types examined, some possible trends were identified. These suggest that a threshold at which over-application of nutrients may inhibit enzyme activity by providing excess supplies was either not reached, or that insufficient time was allowed prior to analysis to allow the inhibitory effects to develop. Even though the litter examined was rich in organic matter, the activity of enzymes involved in C breakdown was low, probably because the increased availability of C reduced their activity efficiency resulting in lower C releases from the litter (Allison *et al.*, 2007). Other studies have shown that reduced enzyme efficiency is often reflected by a compensatory increase in microbial biomass (Allison *et al.*, 2007).

In conclusion, the three litter types degraded at different rates, which was linked, in part, to the C and nutrient status of the litter and the proportions of C and nutrients held in recalcitrant pools compared to labile fractions. Indeed, the measurements of enzyme activity confirmed that litter decomposition at the *Cyperus* sp. site was probably limited by P availability. The relatively low and rapidly depleted semi-labile P pool (shown in the acid extraction) supports this. In addition to nutrient status and litter quality, the level of the water table was an important factor controlling mass loss, with greater decomposition rates being found when the water table was low. These findings highlight the multiple factors involved in controlling decomposition processes and the important role of both

abiotic and biotic variables in determining peat accumulation in this tropical peatland.

Chapter 8 Final discussion and future research

8.1 Introduction

The focus of this study was to investigate carbon dioxide (CO₂) and methane (CH₄) fluxes at three sites with differing dominant vegetation species across a nutrient gradient in the San San Pond Sak peatland in Panama. Specifically to explore the extent of spatial and temporal variation in gas fluxes, and examine the influence of variations in environmental factors on the CO₂ and CH₄ production. The carbon (C) store of tropical peatlands is estimated to be 89 Gt C (Page *et al.*, 2010). The quantification of the fluxes of CO₂ and CH₄ is important in terms of understanding decomposition of peat and the potential accumulation or degradation of the peat deposits (C stores) under future climate scenarios.

Several studies have investigated C cycling in tropical peatlands, with the main body of research focusing on SE Asian systems (Sorensen, 1993; Miyajima *et al.*, 1997; Inubushi *et al.*, 1998; Page *et al.*, 1999, 2002, 2010; Furukawa *et al.*, 2005; Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a, b; Hirano *et al.*, 2009; Jackson *et al.*, 2009; Couwenberg *et al.*, 2010). Comparatively few studies have considered peatlands in Central America (e.g. Phillips *et al.*, 1998; Troxler, 2007; Sjögersten *et al.*, 2010; Wright *et al.*, 2011).

Substantial variation in CO₂ and CH₄ production has been reported between different peatland systems as well as over time. The extent and drivers of this variability need to be understood and quantified to develop a mechanistic understanding of the processes that govern C fluxes within Neotropical peatlands.

The work presented here focuses on different aspects of variability in CO₂ and CH₄ fluxes and decomposition rates. Chapter 4 investigated the variation of *in situ* CO₂ and CH₄ fluxes on intra-annual, inter-annual and

diurnal timescales. Chapter 5 explored the extent of *in situ* spatial variation and the influence of temperature and nutrient manipulations on *ex situ* potential fluxes. Chapter 6 examined CO₂ and CH₄ production throughout the peat profile, both *in situ* and *ex situ*, while Chapter 7 investigated microbial activity and litter decomposition. The present chapter aims to provide a synthesis of the variation in CO₂ and CH₄ fluxes from the San San Pond Sak peatland and evaluate the extent of the influence of environmental variables on gas production and emission. Key findings are presented along with suggestions for future studies.

8.2 CO₂ and CH₄ fluxes; key findings from this study

- CO₂ flux varied temporally, over both short (diurnal) and long (annual) time periods. Notably with increased CO₂ flux between 1200 and 1400 h on diurnal basis and during periods of low rainfall on an annual basis.
- CH₄ flux was found to vary on an annual basis, but no clear pattern of variation was determined. Overall the sites sampled were a source of CH₄ release to the atmosphere.
- CO₂ and CH₄ fluxes varied between sites of different dominant vegetations, this was found to be due to several influencing factors, including; the dominant vegetation species, quality of litter inputs, the nutrient status of the peat and porewater, the moisture status of the peat and microtopography of the sample sites.
- There was evidence found for potential CO₂ and CH₄ production throughout the upper 2 m of the peat profile.

8.3 Temporal variation in CO₂ and CH₄ fluxes

Studies of the variation of *in situ* CO₂ and CH₄ fluxes from the surface of the peat were reported in Chapters 4 and 5. A strong intra-annual variation in CO₂ flux was found for all sites examined (Fig. 5.1) as the lowest CO₂ fluxes in June and July 2007 were c. 30-40 % of those found in February and March 2007. CO₂ fluxes were generally greatest at the *C. panamensis* site and lowest at the *Cyperus* sp. site where the values were c. 50 % of those at the former site.

The significant diurnal variation in CO₂ fluxes observed at the *C. panamensis* and *Cyperus* sp. sites (Fig. 5.7) has important implications for the timing of measurements of CO₂ fluxes as a mean increase of 300 mg CO₂ m⁻² h⁻¹ was recorded between 13:00 and 16:00 h in August 2009. The potential effect that time of sampling may have on measured CO₂ fluxes could partially explain the differences in measured CO₂ fluxes at the *Cyperus* sp. site in August 2007, compared to August 2009 (Figs. 5.1 and 4.3), as the time of day when measurements were made differed between years. Thus, gas fluxes were measured at c. 12:00 h in August 2007 but at c. 14:00 h in August 2009, with the result that the mean CO₂ flux in August 2009 was approximately four times greater than that in August 2007. The time of sampling is only one of several potential factors that could affect the CO₂ flux between years; examples of others are peat moisture status and peat temperature. When considering the diurnal variation pattern (Fig. 5.7c), it seems likely that these values were at least in part affected by the time of sampling, possible to a greater extent than differences between years, as the CO₂ fluxes for *C. panamensis* were measured at similar times in both years and were of comparable magnitude. The observation that diurnal variation in CO₂ fluxes occurred in only two of the three vegetation types examined is consistent with previous literature in that not all locations show such patterns. It is likely that the occurrence of diurnal variation in CO₂ fluxes is in part dependent on the dominant vegetation present (Thomas *et al.*, 1996; Schwendenmann *et al.*, 2003; Hirano *et al.*, 2009). Hence, in order to

accurately determine net CO₂ emissions from peatlands fluxes over both diurnal and seasonal cycles need to be considered.

The San San Pond Sak peatland was found to be an overall source of CH₄ released from the peat surface to the atmosphere, although CH₄ fluxes showed no significant variation with time or site, on neither an annual or diurnal basis (Fig. 5.6), significant variation was seen when the same months of different years were compared, both between years and between sites Fig. 5.13). Water table drawdown was rare in San San Pond Sak, and when it did occur was typically less than 10 cm with a maximum observed water table draw down of 25 cm, these typically flooded conditions would normally promote anaerobic decomposition and hence CH₄ production. This leads to the conclusion that the measured CH₄ fluxes from the peat surface did not reflect the overall production of CH₄ throughout the profile. Fluxes from *in situ* diffusion tubes suggest that CH₄ is being produced at depths at times when it is not occurring in the surface layer (Fig. 6.9 a-c). It may be that CH₄ that is produced at depth is either oxidised or that there may therefore be another pathway of CH₄ release which by-passes the peat surface. Several studies have demonstrated CH₄ uptake and emission by peatland plants (Whiting and Chanton, 1993; Kutzbach *et al.*, 2004; Ding *et al.*, 2005; Furukawa *et al.*, 2005). As CH₄ is produced throughout the profile (Figs. 6.4, 6.9), it is possible that there was substantial CH₄ release from the surface vegetation after entering roots and transport to the shoots through the stem. Indeed preliminary data from the peatland (S. Sjögersten pers. comm.) suggest that CH₄ can be released through *R. taedigera* stems. Another alternative release pathway is ebullition. There is a suggestion of ebullition in San San Pond Sak, where at the *R. taedigera* site occasional CH₄ flux measurements were substantially greater than the majority of measurements, for example 69.9 mg CH₄ m⁻² h⁻¹ measured in September 2007 (Figs. 5.6a, b). Other studies have shown that ebullition makes a significant contribution to CH₄ release (Debusk and Reddy, 2003; Tokida *et al.*, 2005; Laing *et al.*, 2008). Contrary to previous studies (Thomas *et al.*, 1996; Mikkela *et al.*, 1995; Laine, 2007), there was no significant diurnal variation in CH₄ surface flux (Fig. 5.10). It is worth noting however

the small number of replicates and repeats, thus it might be that subtle differences could be detected with more comprehensive measurements.

8.4 Rainfall and hydrology

8.4.1 CO₂ and CH₄

CO₂ fluxes were found to vary quadratically with cumulative rainfall for the 28 days prior to sampling (Fig. 5.5). This occurred across all sites and accounted for 22, 31 and 26 % of the variation in CO₂ flux at the *R. taedigera*, *C. panamensis* and *Cyperus* sp. sites respectively. Cumulative rainfall is used as an indication as to the likely moisture status of the peatland, i.e. at higher cumulative rainfall the more likely it is that the peatland is saturated or flooded. The quadratic relationship was unexpected and is likely due to co-variation in other environmental variables e.g. NPP rather than the cumulative rainfall itself. The majority of peatland studies have found a relationship between the water level relative to the peat surface and the CO₂ flux which suggests that CO₂ flux increases with water level drawdown (Oechel *et al.*, 1993; Silvola *et al.*, 1996; Debusk and Reddy, 2003; Furuwaka *et al.*, 2005; Jauhiainen *et al.*, 2005). In this study a positive linear relationship was found over water levels ranging from -6 cm to +6 cm, with CO₂ fluxes ranging from c. 20 - 950 mg m⁻² h⁻¹. The continued increase in CO₂ flux under relatively higher water levels is comparable to results found in other tropical peatlands, for example, Hirano *et al.*, (2009) found that the CO₂ flux from the surface of hummocks in an Indonesian peatland did not begin to decrease until the water levels were greater than 10 cm above the surface. This suggests that there is a sufficient supply of oxygen to the peat either by diffusion of oxygen, or by plant root inputs of oxygen into the peat to enable oxic conditions when the water level is < 10 cm above the peat surface. There was no correlation of CH₄ with either cumulative rainfall or water level, which further supports the suggestion that either the peat conditions were oxic and so unfavourable to CH₄ production (and concurrently favourable to oxidation in the surface layer) or that CH₄ is released *via* an alternative pathway. These conclusions are based on the well documented link

between CH₄ production and water level relative to the surface of the peat which typically occurs at water tables around the peat surface. (Furuwaka *et al.*, 2005; Jauhiainen *et al.*, 2005, 2008; Laine *et al.*, 2007; Dinsmore *et al.*, 2009; Couwenberg *et al.*, 2010).

8.4.2 Litter decomposition

The importance of hydrology on litter decomposition was studied in two mass loss experiments. Both *C. panamensis* and *Cyperus* sp. litters showed greater mass losses, 44 and 33 %, respectively, at unsaturated conditions while decomposition of the *R. taedigera* litter was not affected by the water level. The initial composition of the litter fractions suggests that the carbon substrate availability was similar for each litter type, with similar percentages of labile and recalcitrant fractions (Fig. 7.2). C:N ratios as a predictor of decomposition rate were contrary to the relationship often suggested in other studies, that a high C:N ratio indicates a low decomposition rate, as *C. panamensis* litter had the highest initial C:N ratios of c. 26 - 32 (Fig. 7.4a), yet had the greatest decomposition rate of the three litter types.

The difference in the decomposition patterns of the three litter types suggest that the rate of nutrient inputs at the three sites differs with potential implications for the microbial communities. It also suggests that the decomposition rates were not limited by the lability of the organic C in the litter, but rather by phosphorus, as suggested by the rapid loss of phosphorus from labile and semi-labile fractions of the litter between weeks 0 and 1 for all litter types and water levels (Rejmankova, 2001; Sayer *et al.*, 2006).

The importance of hydrology for C cycling in tropical peatlands is highlighted in this study, however the majority of measurements investigated in this study were taken when water level was between -10 cm and +10 cm relative to the peat surface and hence do not indicate the potential impacts on carbon and nutrient cycling of either substantial water table drawdown or flooding events.

8.5 Effects of carbon and nutrient availability

8.5.1 *R. taedigera* site

Decomposition at the *R. taedigera* site is potentially limited by the availability of labile carbon substrates. This is suggested by the positive correlation between DOC and CO₂ flux (Fig. 4.9a), in combination with substantial losses from the labile and recalcitrant carbon fractions of the litter (Fig. 7.3a, b; 7.5a, b; 7.7a, b). The slow rate of *R. taedigera* litter decomposition relative to other litter studies, also suggests that there is a limitation on microbial communities. The *R. taedigera* litter had the highest initial concentrations of labile phosphorus (0.013 % of total sample mass) and labile nitrogen (0.72 % of total sample mass) suggesting that the availability of nutrients is the least likely to be limited, compared to the *C. panamensis* and *Cyperus* sp. sites. Enzyme assays on peat samples found that there was a high cellobiohydrolase activity relative to the other sites. Cellobiohydrolase produces extracellular enzymes involved in the decomposition of carbon substrates, and the high activity rate suggests that there is a substantial labile C pool (Jackson *et al.*, 2009).

8.5.2 *C. panamensis* site

C. panamensis peat generally had the greatest flux of CO₂ (100 - 400 mg m⁻² h⁻¹; Fig. 4.1) and the greatest initial organic matter loss (c. 35 %). The high flux and organic matter loss suggest that this site would have the lowest carbon accumulation rates if equal quantities of litter inputs are assumed. The positive correlation of dissolved carbon to dissolved phosphorus (DC:DP) and dissolved nitrogen (DN) to DP (DN:DP) ratios with CO₂ flux suggest that increased phosphorus concentrations may decrease decomposition processes. This is contrary to the findings in the majority of litter studies (for example, Rejmankova, 2001) which suggest that increased P availability should increase the rate of decomposition

when P is limiting. This was seen in the positive correlation of CH₄ fluxes with DP and also DOC and DN. However, as discussed earlier it is likely that the CH₄ measured in this study was not an accurate representation of the production of CH₄ within this peatland. As such any correlation of CH₄ with environmental variables is of dubious reliability when considering the relationship as representative of the peatland system, rather than representative of the fluxes from the peat surface.

The data collected at this site suggests that there is neither C, N or P limitation on decomposition processes at this site. It is possible that the apparent relationship between high P and low CO₂ flux is due to a factor other than P availability that is affecting CO₂ production. For example, Freeman *et al.*, (2004) found that when there was lower phenol oxidase activity there was a subsequent accumulation of humic acid within the peat which inhibited the activity of hydrolase enzymes. These conditions could potential lead to decreased gas production and accumulation of C and nutrients.

8.5.3 *Cyperus sp.* site

Fluxes at the *Cyperus sp.* site were not correlated with either carbon or nutrient factors. The relatively high activities of all enzymes measured at this site suggests that the availability of labile carbon and nutrients is low, particularly P as indicated by the < 0.01 mg l⁻¹ DP in the surface water. The labile P concentration in the *Cyperus sp.* litter was the lowest of all the litter types, the low DP of the surface water, in combination with the rapid depletion of P seen in the labile and semi-labile fractions as demonstrated in the litter decomposition study over weeks 0 to 1 (Fig 7.3; 7.5).

8.5.4 Depth effects

8.5.4.1 *In situ* fluxes

In situ measurements found that CO₂ and CH₄ were produced throughout the first 1 m of the peat profile. This implies that there are oxic and anoxic

zones within the peat that enable CO₂ and CH₄ to be produced concurrently (Fig. 6.8; 6.9). The *in situ* CH₄ flux rates found suggest that the degree of aeration of the peat can vary. In July 2009 CH₄ production was predominately occurring at > 30 cm depth, this implies that any CH₄ that diffused through the peat profile and passed into an aerated surface layer would be oxidised by methanotrophic bacteria. It is possible that CH₄ produced within the profile was released *via* an alternative pathway, such as, *via* uptake by the roots of vegetation. However in August 2009 there was found to be CH₄ flux from the peat surface to the atmosphere. From this it can be inferred that conditions in the surface layer (< 30 cm depth) can vary as to the degree of aeration. This has implications for the extent of CH₄ oxidation in the surface layer and to what degree this affects future CH₄ fluxes.

8.5.4.2 *Ex situ* fluxes

Ex situ fluxes indicate that there was potential for CO₂ and CH₄ production through the upper peat profile (Fig. 6.10). This indicates the partially decomposed nature of the peat, as there is sufficient substrate and nutrient availability, at depths beyond the rooting zone, to support microbial communities. This is also supported by the relatively high dissolved carbon and nutrient contents, indicating the presence of labile substrates through the profile (Fig. 6.7). The relatively lower C:P, C:N and N:P ratios of the surface indicate that this is the most likely zone of potential decomposition. The increase in ratios by depths of c. 40 - 60 cm indicate that decomposition rates will be slower at depth compared to the surface decomposition rates.

The concentration of P declines rapidly from 0 to 40 cm depth (Fig. 6.5c), whereas C and N are fairly consistent with a slight decreases with depth. This indicated that P may be limiting decomposition at depths within the profile as P is utilised in the surface zone, where the greatest rates of microbial activity are typically seen (Jackson *et al.*, 2009).

The *in situ* and *ex situ* fluxes indicate that although the surface layer is often the most active zone of a peatland (as was the case in this study),

likely due to fresh litter inputs and therefore the greatest availability of C and nutrients to microbial communities, production of CO₂ and CH₄ still occurs throughout the profile. This has important implications when considering fluxes under potential water drawdown under changing climate and suggests a possible substantial increase in CO₂ fluxes. It was not possible to predict the effect of water table drawdown on CH₄ fluxes based on the results of this study.

8.6 Overall conclusions on CO₂ and CH₄ fluxes from San San Pond Sak

The fluxes of CO₂ and CH₄ were investigated with the aim of quantifying their variation and the influence of environmental variables on the flux rate. CO₂ fluxes varied in magnitude between sites, but had the same general pattern, with the lowest fluxes during wet seasons and greatest fluxes during dry seasons. This suggests that the influence of seasonal changes in environmental factors had similar effects on fluxes at all site, regardless of the dominant surface vegetation, when considered on an annual basis.

When the sites were studied separately, the differences that were attributed to the surface vegetation species were more apparent. The *R. taedigera* dominated site had no diurnal variation in CO₂ or CH₄ flux, suggesting that the vegetation rate of photosynthesis did not have an effect on the gas production *via* root inputs of substrates or oxygen into the peat profile, whereas *C. panamensis* and *Cyperus* sp. sites were found to have CO₂ diurnal fluxes that followed the circadian rhythm of plant processes. The *R. taedigera* site is suggested to be limited by the availability of carbon substrates, inferred from the slow rate of decomposition, fairly rapid carbon losses from labile and recalcitrant fractions compared to *C. panamensis* and *Cyperus* sp. litters and the positive correlation of DOC and CO₂ flux.

At the *C. panamensis* site findings suggest that fluxes were substantially influenced by dissolved C and nutrients. The *C. panamensis* litter had rapid initial decomposition, which suggests a high labile C and nutrient pool at this site relative to *R. taedigera* and *Cyperus* sp. sites. It is likely that this site would be the most sensitive of the three to nutrient inputs, such as, high litter deposition due to storm events (Ostertag *et al.*, 2003).

The CO₂ fluxes at the *Cyperus* sp. site varied with cumulative rainfall in the 28 days prior to gas sampling, the line of best fit described a quadratic relationship that explained 26 % of the CO₂ variance. Diurnal variation in CO₂ flux similar to the circadian rhythm of the surface vegetation, suggest that factors influencing the photosynthetic rate of the vegetation will have a subsequent effect on the CO₂ production within the peat. The highest enzyme activity was found at the *Cyperus* sp. site suggesting that possibly C, N or P availability (or a combination) in a labile form was limiting at this site.

In conclusion, whilst there was a similar annual pattern of CO₂ flux variation across the three sites, the environmental factors that control the magnitude of this flux may vary from site to site dependent on the dominant vegetation species.

CH₄ fluxes were not found to vary systematically on either annual or diurnal timescales. Within site variation was partial explained at the *C. panamensis* site by the concentrations of DOC, DN and DP in the surface water.

8.7 Comparison of the CO₂ and CH₄ flux rates of San San Pond Sak with other tropical peatlands and implications for future CO₂ and CH₄ flux measurements

CO₂ fluxes found in this study are comparable with those found in other tropical peatlands (Jauhiainen *et al.*, 2005; Melling *et al.*, 2005a). Although some peatlands of SE Asia have been found to produce CO₂

fluxes of a greater magnitude than those found in San San Pond Sak (typically $< 600 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), for example, Melling *et al.* (2005a), found CO_2 fluxes of up to $1953 \text{ mg m}^{-2} \text{ h}^{-1}$ in a mixed peatswamp forest of Sarawak Malaysia. Hirano *et al.* (2009) found CO_2 fluxes of up to $950 \text{ mg m}^{-2} \text{ h}^{-1}$ in a peatswamp forest in Centreal Kalimantan, Indonesia. However the high CO_2 fluxes found in these two studies were measured in peatlands that experienced a greater degree of WT drawdown than that seen in San San Pond Sak. In the study by Melling *et al.* (2005a) the WT drawdown was 100 cm below the peat surface at the time of the highest CO_2 flux. Similarly, in the study undertaken by Hirano *et al.* (2009) the higher CO_2 fluxes measured in hummocks occurred when the WT drawdown was $> 25 \text{ cm}$ below the surface at the time of measurement. Therefore it is likely that CO_2 fluxes from San San Pond Sak would be comparable to, if not greater than those of SE Asia if the WT drawdown was as extensive. The potential CO_2 fluxes measured in the laboratory during this study also support this hypothesis, with potential surface layer emissions of *ca.* $820 - 1550 \text{ mg m}^{-2} \text{ h}^{-1}$.

In the future San San Pond Sak is expected to become drier and warmer if the climate changes as is currently predicted (Giorgi, 2006; Baettig *et al.*, 2007; IPCC 4AR, 2007; Solomon *et al.*, 2008). This is likely to result in WT drawdown beyond that seen currently (typically $< 25 \text{ cm}$ below the surface), initially CO_2 fluxes under WT drawdown would likely exceed those of SE Asia, the measured high potential fluxes and the high availability of labile C at depths of up to 2 m (*cf.* section 6.3) would potentially result in large CO_2 emissions as the profile first becomes aerated that would be expected to decrease in magnitude over time as the C stores are depleted and not replaced (Hooijer *et al.*, 2010).

At the other end of the range, the lower CO_2 fluxes measured in San San Pond Sak (lower fluxes classed at those $< 50 \text{ mg m}^{-2} \text{ h}^{-1}$) were lower than those typically found in other tropical peatlands, the majority of studies in comparable peatlands typically found CO_2 fluxes greater than $100 \text{ mg m}^{-2} \text{ h}^{-1}$ (Chimner, 2004; Melling *et al.*, 2005a; Hirano *et al.*, 2009; Sjogersten *et al.*, 2010). This is an indication that the flooding in San San Pond Sak is

likely to be more extensive than that of other tropical peatlands, as lower CO₂ fluxes are typically associated with higher WTs that create conditions unfavourable for aerobic decomposition.

CH₄ fluxes found in tropical peatlands vary greatly. Compared to other tropical peatlands the majority of CH₄ effluxes measured in San San Pond Sak were found to fall in the range 0 – 1 mg m⁻² h⁻¹. This is similar to a CH₄ efflux of 1.1 mg m⁻² h⁻¹ found in a swamp forest in Indonesia by Innubushi *et al.* (1998). However other tropical peatlands had lower CH₄ efflux, for example, Jauhiainen *et al.* (2005) found < 0.35 mg m⁻² h⁻¹ in a swamp forest peatland in Central Kalimantan. Melling *et al.* (2005b) found a CH₄ efflux of < 0.011 mg m⁻² h⁻¹ in a mixed peatswamp forest of Sarawak, Malaysia.

The higher point effluxes found in this study (for example, 69.9 mg CH₄ m⁻² h⁻¹ at the *R. taedigera* site) thought to be due to bubble ebullition were much greater in magnitude than those of comparable tropical peatlands and were on a par with the magnitude of fluxes measured in rice paddies (Furukawa *et al.*, 2005; Hadi *et al.*, 2005).

Although CH₄ efflux is typically associated with flooded conditions, in this study CH₄ efflux was measured even when there was WT drawdown. This has also been found in other studies of tropical peatlands (Jauhiainen *et al.*, 2005; Melling *et al.*, 2005b; Sjogersten *et al.*, 2011). Melling *et al.* (2005b) found that CH₄ effluxes ceased when WT drawdown was > 65 cm below the peat surface and uptake of CH₄ occurred instead.

In regards to future climate change predictions CH₄ efflux would be expected to eventually cease if the climate of San San Pond Sak becomes increasingly warmer and drier thereby increasing the WT drawdown in this location creating conditions unfavourable to anaerobic decomposition.

8.8 Implications for future studies

This study has established highly variable CO₂ and CH₄ fluxes at the study site. This has implications for other studies in ensuring that the number of replicate measurements cover the variation in microtopography of the peat surface, to enable accurate estimations of peatland fluxes. This is valid for both temporal and spatial variation in gas fluxes.

The importance of the surface dominant vegetation species with regards to CO₂ and CH₄ flux has implications for the up-scaling of field measurements to large areas. The vegetation species would need to be accurately estimated by surface area covered and fluxes sampled at each site of differing dominant vegetation to ensure an accurate reflection of the peatland total flux.

The measurement of CH₄ flux has indicated the importance of considering release pathways other than the peat surface, particularly *via* root uptake and release by vegetation.

8.9 Future research directions

- CH₄ flux was not found to vary with hydrological factors in this study. Based on the strong relationships found in studies in comparable systems it is possible that in addition to surface emissions CH₄ fluxes may be released *via* pathways other than the peat surface i.e. the vegetation. To improve the estimations of CH₄ flux in this peatland, releases *via* the surface vegetation should be quantified.
- The peat surface CO₂ flux reported in this study was a combination of root respiration and microbial respiration. Future studies should look to separate root respiration from microbial respiration to provide a more accurate estimate of carbon losses *via* decomposition processes in this peatland.

- As root respiration potentially contributes a significant portion of the CO₂ flux to the atmosphere, the influence of rooting biomass, coarse and fine roots contributions and root turnover times should be studied to allow quantification of the contribution of rooting systems of different vegetation species to the surface CO₂ flux.
- CO₂ and CH₄ production were found to occur concurrently through the peat profile. Future studies should aim to investigate the redox potential through the profile to provide a more detail picture of the extent of oxic/anoxic conditions with the peat and therefore the potential extent of CO₂ and CH₄ production.
- The effect of nutrient manipulations on the microbial activity of peat from this study was inconclusive. Future studies should aim to determine the response of microbial communities to changes in environmental variables, with particular regards to water table, C and nutrient inputs and temperature to enable predictions of the microbial community response to climate change and the subsequent impact on CO₂ and CH₄ production.
- This study found differing patterns of litter decomposition between species, further to this the times and magnitudes of litter deposition events should be studied to increase knowledge of the carbon and nutrient inputs into the peat and how these differ between sites of differing dominant vegetation species.

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Contribution of subsurface peat to CO₂ and CH₄ fluxes in a neotropical peatland

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Abstract

Tropical peatlands play an important role in the global carbon cycling but little is known about factors regulating carbon dioxide (CO₂) and methane (CH₄) fluxes from these ecosystems. Here, we test the hypotheses that (i) CO₂ and CH₄ are produced mainly from surface peat and (ii) that the contribution of subsurface peat to net C emissions is governed by substrate availability. To achieve this, *in situ* and *ex situ* CO₂ and CH₄ fluxes were determined throughout the peat profiles under three vegetation types along a nutrient gradient in a tropical ombrotrophic peatland in Panama. The peat was also characterized with respect to its organic composition using ¹³C solid state cross-polarization magic-angle spinning nuclear magnetic resonance spectroscopy. Deep peat contributed substantially to CO₂ effluxes both with respect to actual *in situ* and potential *ex situ* fluxes. CH₄ was produced throughout the peat profile with distinct subsurface peaks, but net emission was limited by oxidation in the surface layers. CO₂ and CH₄ production were strongly substrate-limited and a large proportion of the variance in their production (30% and 63%, respectively) was related to the quantity of carbohydrates in the peat. Furthermore, CO₂ and CH₄ production differed between vegetation types, suggesting that the quality of plant-derived carbon inputs is an important driver of trace gas production throughout the peat profile. We conclude that the production of both CO₂ and CH₄ from subsurface peat is a substantial component of the net efflux of these gases, but that gas production through the peat profile is regulated in part by the degree of decomposition of the peat.

Keywords: carbon, methane, nutrient gradient, Panama, peatland, solid state ¹³C CPMAS NMR, tropical

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Introduction

Tropical peatlands are known to have considerable significance in the global carbon (C) cycle (Page *et al.*, 2011; Vegas-Vilaruba *et al.*, 2010), but the sink strength of tropical peatlands is under increasing threat from changes in land use and climate (Couwenberg *et al.*, 2010). In areas of the tropics which are expected to experience reduced rainfall and more prolonged drought (Meehl *et al.*, 2007), peatlands may become less important sources of atmospheric methane (CH₄). However, this would be offset by greatly increased rates of aerobic decomposition and carbon dioxide (CO₂) release, with the result that their combined global warming potential would increase (Hirano *et al.*, 2009; Couwenberg *et al.*, 2010; Sjögersten *et al.*, 2010). It is

also plausible that old C stored deep in the peat profile would be metabolized if climatic conditions become more favourable for decomposition, as has been reported for northern peatlands (e.g. Dorrepaal *et al.*, 2009). In tropical environments, a substantial draw down of the water table would be required to impact deep peat layers.

Considerable variation in C fluxes occurs between vegetation types in tropical wetland systems (Melling *et al.*, 2005a, b; Sjögersten *et al.*, 2010), suggesting that C inputs from the vegetation (Sebacher *et al.*, 1985; Joabsson & Christensen, 2001; Konnerup *et al.*, 2010) are strong drivers of C fluxes in these systems. However, it is not known if these differences in C fluxes result mainly from surface processes or are maintained throughout the peat profile. Tropical peatlands may reach depths of up to 15 m (Phillips *et al.*, 1997; Page *et al.*, 1999, 2004; Shimada *et al.*, 2001; Hope *et al.*, 2005). To date, most studies of C fluxes from such systems

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have focused on surface fluxes of CO₂ and CH₄ (e.g. Jauhainen *et al.*, 2005; Hirano *et al.*, 2007; Sjögersten *et al.*, 2010), but little is known about the factors influencing the production and emission of these gases. Greater CH₄ production at depth (at least down to 50 cm) than in surface peat has been noted in peatlands in Sarawak, Malaysia (Inubushi *et al.*, 1998) and CH₄ production at 80 cm depth has been found to vary over several orders of magnitude between vegetation types (Melling *et al.*, 2005a).

Paleoecological studies of the Changuinola peat deposit on the Caribbean coast of western Panama demonstrated variation in the dominant peat-forming vegetation over a period of ca. 4500 years and changes in peat structure with depth (Phillips *et al.*, 1997). These observations suggest that the degree of peat decomposition and properties vary not only over the surface of peatlands (Sjögersten *et al.*, 2010) but also with depth, as has also been shown in higher latitude peatlands (Krull *et al.*, 2004; Forbes *et al.*, 2009; Grover & Baldock, 2010). In these systems, there is a trend for higher aliphatic to carbohydrate ratios (commonly used to indicate the degree of decomposition; Baldock & Preston, 1995) and more aromatic compounds to be found at depth, consistent with an increasing degree of decomposition with depth. Such changes in peat composition with depth have implications for microbial degradation of C stored in peatlands; for example, Grover & Baldock (2010) demonstrated a link between peat substrate quality and mass loss, with lower decomposition rates being found in the deeper peat deposits. Indeed, the supply of labile C limits heterotrophic microbial activity in the surface layers of tropical, subtropical and boreal peatlands (Miyajima *et al.*, 1997; Bergman *et al.*, 1999; Wright *et al.*, 2009), with implications for the production of CO₂ and CH₄ throughout the peat profile.

In northern peatlands, there is good evidence that the contribution of old C from depths ≥ 4 m to surface gas efflux is low (Charman *et al.*, 1994, 1999; Chanton *et al.*, 1995, 2008; Garnett & Hardie, 2009). In agreement with this observation, microbial activity in tropical peatlands has been shown to decline with depth based on studies of microbial enzyme activity (Jackson *et al.*, 2009), although it is unclear how this translates into CO₂ and CH₄ effluxes from different peat layers formed under contrasting vegetation types. Furthermore, root activity impacts on CO₂ and CH₄ fluxes throughout the peat profile by influencing belowground O₂ supplies (e.g. Dinsmore *et al.*, 2009; Fritz *et al.*, 2011) and substrate inputs (e.g. Laing *et al.*, 2010), and by allowing rapid transport of CH₄ through the roots to the surface, thereby avoiding oxidation within the peat profile (e.g. Purvaja *et al.*, 2004; Chen *et al.*, 2010). In northern peatlands, CH₄ production has been associated with distinct

subsurface peat layers, with emissions being much lower for the intervening layers (Laing *et al.*, 2010; Shoemaker & Schrag, 2010). In addition to such vertical variation in gas production, spatial variability in nutrient availability (Koelbener *et al.*, 2010) and forest composition controls gas transport (Konnerup *et al.*, 2010) and shapes microbial activity in the surface peat layers in tropical peatlands. Gas fluxes vary substantially between vegetation types (Chimner, 2004; Melling *et al.*, 2005a,b; Sjögersten *et al.*, 2010), in parallel with the substantial variation between species with respect to gas transport demonstrated recently in tropical wetland plants (Konnerup *et al.*, 2010). Together, this evidence points towards substantial variation in gas production throughout the profile in relation to variation in substrate availability and the physiochemical environment.

In this paper, we explore variation in peat properties and associated gas fluxes throughout the profile at three sites in a neotropical peatland with distinct vegetation communities to test the hypotheses that: (i) CO₂ and CH₄ are produced mainly from surface peat and; (ii) the contribution of subsurface peat to net C emissions is governed by substrate availability. To test these hypotheses, CO₂ and CH₄ fluxes from different peat layers were measured both *in situ* and *ex situ* in an ombrotrophic domed tropical coastal peatland in western Panama. Gas fluxes were then correlated with substrate composition throughout the peat profile determined using solid state ¹³C cross-polarization magic-angle spinning nuclear magnetic resonance (CPMAS NMR).

Materials and methods

Site description

The San San Pond Sak peatland is a 164 km² mosaic of freshwater and marine-influenced wetlands in Bocas del Toro Province on the Caribbean coast of western Panama (Cohen & Stack, 1996). Recognized internationally as a site of special scientific interest (Ramsar site #611), it includes the significant 80 km² Changuinola peat deposit, an ombrotrophic domed peatland to the south east of Changuinola river.

The oldest deposits in the Changuinola peatland are estimated to have been formed 4000–4500 years ago and are >8 m deep in the central areas (Phillips *et al.*, 1997). Peat at the edges of the peatland is younger and ca. 2 m deep. The vegetation communities which formed the peat have shifted spatially over time, meaning that C inputs and environmental conditions at specific locations have differed greatly (Phillips *et al.*, 1997). The texture of the peat varies between the interior, where it is predominantly coarse to a depth of 2–4 m and dominated by roots in the surface layers, to the edges where the peat has a fine texture throughout the profile (Phillips *et al.*,

1997), indicating greater decomposition and/or differences in the source of litter.

Seven distinct phasic plant communities cover the peatland in approximately concentric rings (Phillips *et al.*, 1997). Starting from the periphery, these communities have been designated as (i) *Rhizophora mangle* mangrove swamp, (ii) mixed back mangrove swamp, (iii) *Raphia taedigera* palm swamp, (iv) mixed forest swamp, (v) *Campnosperma panamensis* forest swamp, (vi) sawgrass/stunted forest swamp and (vii) *Myrica-Cyrilla* bog-plain. Nutrient levels in the peat and plant tissue vary greatly between vegetation communities and are generally low in the interior and higher towards the edge of the peatland (Troxler, 2007; Sjögersten *et al.*, 2010). Previous work has shown that the low nutrient content in the interior is reflected by lower microbial biomass C:N and C:P ratios and upregulation of the activity of extracellular enzymes involved in nutrient acquisition (Sjögersten *et al.*, 2010). Furthermore, *in situ* CO₂ and CH₄ fluxes did not appear to reflect nutrient availability, while drained surface peat samples exhibited lower CO₂ production in material from the interior than sites closer to the edge of the peatland (Sjögersten *et al.*, 2010).

The nearby town of Bocas del Toro, Isla Colon, ca. 10 km from the peatland, has a mean annual temperature of 27 °C with low intra-annual variability and a mean annual precipitation of 3209 mm between 1992 and 2001 (Estadística Panameña, 2001). Rainfall is continuous throughout the year with no pronounced dry season, although there are two distinct periods of lower rainfall (February–April and September–October). The water table is generally at the surface of the peatland throughout the year, with no distinct period of draw

down. Mean peat temperature 10 cm below the surface is ca. 25 °C and shows little intra-annual variation (E. L. Wright *et al.*, unpublished data).

Experimental programme

Two approaches were used to investigate peat characteristics and CO₂ and CH₄ fluxes throughout the profile: (i) *in situ* monitoring of fluxes from the surface and at three depths within the profile and; (ii) *ex situ* incubation of peat from different depths.

Depth profiles of gas fluxes and peat cores were collected along a ca. 2.7 km transect across the peatland for three of the phasic communities identified by Phillips *et al.* (1997). The three communities examined were located near the edge of the peatland (82°24'6.17"W, 9°25'29.50"N), half-way to the central bog plain (82°24'22.61"W, 9°25'13.48"N), and at the edge of the central bog plain (82°24'47.70"W, 9°24'44.31"N) (Fig. 1). The sampling sites were dominated by the following species: *R. taedigera* (Palmae) (palm swamp), *C. panamensis* (Anacardiaceae) (forest swamp) and *Cyperus* sp. (Cyperaceae) (sawgrass plain; cf. Sjögersten *et al.* (2010) for further details of locations and vegetation composition).

In situ gas flux measurements

In situ gas fluxes were determined for the peat surface and at depths of 30, 60 and 100 cm to determine the contribution of surface and deeper peat layers to net CO₂ and CH₄ emissions. Measurements were made for all sites in July 2009, representing the onset of a period of increased rainfall, and August

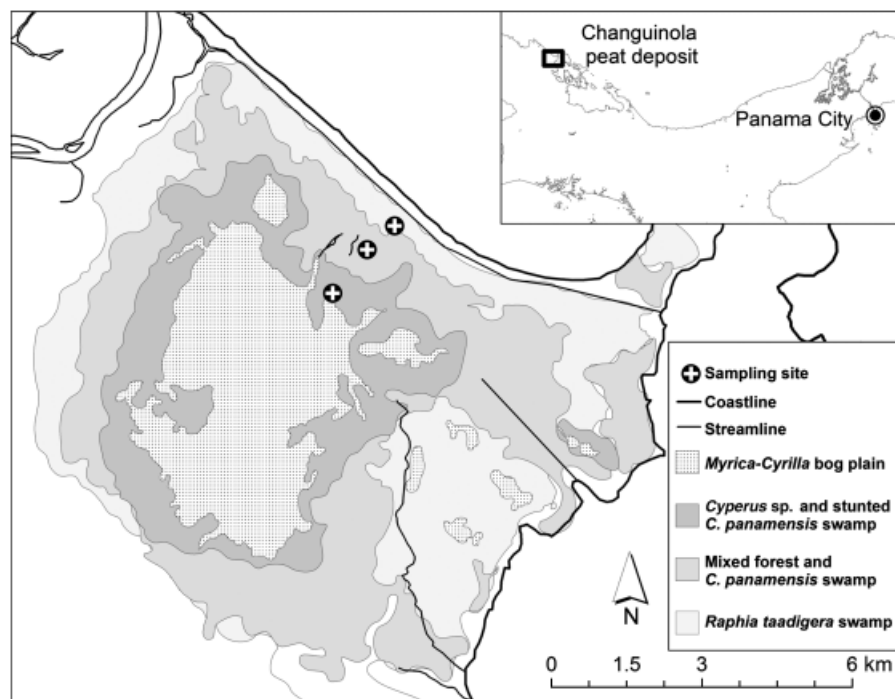


Fig. 1 Map of the Changuinola peat deposit, a portion of the San San Pond Sak wetland, in Western Panama. The dominant vegetation zones (reworked from Phillips *et al.*, 1997) and locations of the three sampling sites are shown; the *Raphia taedigera* site is closest to the coast, followed by the *Campnosperma panamensis* site and the *Cyperus* sp. site towards the centre of the peatland.

2009. Sampling locations at each site were located in four replicated blocks spaced at 20–30 m intervals with four gas sampling depths. The distance between sampling tubes within each block was 50 cm. The total number of plots was 48, comprising three vegetation types, four sampling depths and four replicates. In this method, the gas samples collected from the tubes to estimate gas fluxes are assumed to originate from a vertical column below the sampling tube. However, a proportion of the measured gas flux is likely to have originated from a wider area around the base of the tubes, possibly resulting in overestimation of the true gas production.

In situ gas fluxes were measured using diffusion tubes constructed from 5 cm diameter drainage pipes, open at both ends to allow gas emitted from the peat horizon at the bottom of the tube to migrate up through the water column within the tube. The tubes were inserted using a 3.8 cm diameter borer, which was pushed into the peat to the correct depth before inserting the sample tube over the borer. The tubes protruded 30 cm above the peat surface. When the borer was removed from inside the diffusion tubes, these were emptied of peat but filled rapidly with water. The diffusion tubes were covered with ventilated caps to allow gas exchange with the external atmosphere and ensure leaf material did not enter the tubes; they were then left to equilibrate for eight months. Gas samples were collected by attaching a 5 cm tall opaque head space to the diffusion tubes, giving a total volume of 0.69 dm³; a small fan ensured mixing of the head space air. Twenty-five milliliter samples of air were collected *via* a Suba-Seal[®] (Fisherbrand, Loughborough, UK) using a syringe 0, 2, 10 and 20 min after fitting the head space before transferring these to prepared 12 mL vacuumed exetainers (Labco, High Wycombe, UK). Surface gas samples were collected using a 10 cm tall head space with a volume of 0.45 dm³ placed directly on the peat surface at times 0 and 10 min; the sampling time was adjusted to account for the smaller head space (Yao *et al.*, 2009). All samples were shipped to the University of Nottingham for CO₂ and CH₄ analysis. As an overpressure was injected into the vials, it was easy to detect any loss of sample during transport; samples were discarded when this occurred (<2%). The samples from each head space were checked for linearity before the gas flux calculations.

Concurrently with removal of the peat cores in November 2007, surface CO₂ and CH₄ fluxes were measured in the field for comparison with the *ex situ* data. The sampling technique described above was again used, but with a larger head space volume of 7.8 dm³. Before sampling, the vegetation was carefully removed from the plots where necessary (mainly at the interior *Cyperus* site) by severing it at ground level, while roots and pneumatophores were left in place; removal of the above-ground vegetation may have resulted in underestimation of CH₄ and CO₂ emissions. Air samples (25 mL) were again collected using a syringe 0, 2, 10 and 20 min after placing the head space on the peat surface (Sjögersten *et al.*, 2010). Samples were taken from five plots situated at least 20 m apart for all three sites close to where the peat cores were collected and the diffusion tubes were installed. The depth of the water table was recorded within each diffusion tube relative to the ground surface using a ruler, and peat temperature was measured using a digital thermometer inserted to 10 cm depth in each block.

CO₂ and CH₄ concentrations were analysed simultaneously using a gas chromatograph (GC-2014, Shimadzu, Milton Keynes, UK) fitted with a flame ionizing detector for CH₄ and a thermal conductivity detector for CO₂. The GC was fitted with a 1 mL sample loop and a molecular sieve column.

Peat coring for ex situ measurements

Four 1 m long cores were taken at all three sampling sites, one of which was subsequently extended to a depth of 2 m; each core was located at least 20 m from neighbouring cores. The cores were taken using a simplified lightweight 7.6 cm internal diameter piston corer (Fisher *et al.*, 1992) designed to remove intact undisturbed cores using a vacuum to minimize compaction and ensure that the sampled material remained in the corer during recovery. After collection, the cores were kept upright and stored overnight at 4 °C. On the day after sampling, the cores were subdivided into 10 cm segments which were capped to avoid oxidation of the peat. The segments were allowed to settle and equilibrate at 24 °C for 2 h before sampling. Because of the disturbance of the loose surface layer, the 0–30 cm horizon was regarded as one mixed segment for determination of peat properties and separate 10 cm long surface cores were collected in the field.

Ex situ CO₂ and CH₄ flux measurements

CO₂ and CH₄ fluxes from each core segment were measured by head space analysis at 24 °C and as close to the *in situ* water content as possible. As removal of up to 2 m of hydraulic head increased the diffusion rate of gas through the peat, the *ex situ* gas flux measurements must be regarded as maximum potential rates. Owing to the disturbance of the 0–30 cm layer, CO₂ and CH₄ fluxes from this layer were not included in the analysis; instead, the separately collected 0–10 cm surface peat cores were used to determine surface CO₂ and CH₄ fluxes. Gas sampling was achieved by fitting a head space as described previously and immediately flushing this with nitrogen gas for 20 s to avoid oxidation of the peat; the core segments were left to stabilize for 30 min before sampling. Samples were collected 0 and 10 min after fitting the head space and injected into exetainers as described above. Gas fluxes from the *ex situ* sampling analyses were expressed on both a mass and land area basis to evaluate gas production in relation to: (i) the mass of peat (i.e. mass based) and (ii) the net contribution of each peat layer to surface fluxes (i.e. area based). Cumulative fluxes through the peat profile (single cores to a depth of ca. 2 m) were calculated from the *ex situ* measurements by summing the fluxes from each peat layer.

Determination of peat characteristics

Redox potential was determined for each core segment using a KDCMPtB11 redox probe (Thermo Electron Corporation, Altrincham, UK) before gas sampling. The probe was carefully inserted ca. 3 cm into the peat and allowed to stabilize for 5 min before completing the measurement. Note that redox potential is hard to determine accurately in *ex situ* heterogeneous samples hence these results must be treated with some caution. After determining gas fluxes, the individual segments of the peat cores were mixed and roots and organic fragments

>1 mm were removed. Living roots were separated by their colour and condition and all recovered material was rinsed in deionized water and air-dried. Moisture content was calculated for fresh subsamples by gravimetric loss after 70 h at 70 °C, while pH was determined using a 2:1 fresh peat:deionized water ratio and glass electrode. Bulk density (BD) was determined by recording the fresh weight of each 10 cm peat segment and calculating its dry weight using a wet-dry weight conversion factor based on the moisture content of a subsample from each segment. BD was calculated by dividing the dry peat weight by the sample volume. Organic matter content was estimated from loss on ignition (LOI) after ashing 250 mg of ground air-dried material at 550 °C for 4 h in borosilicate scintillation vials. Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were measured in water samples collected using 10 cm long Rhizon samplers constructed from hydrophilic porous polymer with a pore diameter of ca. 0.1 µm to exclude soil particles (Rhizosphere Research Products, Wageningen, The Netherlands). Samples were frozen during storage and transport and were subsequently analysed using a TOC-V/TN analyser (Shimadzu Corp, Kyoto, Japan). The total C content of the samples was measured by combustion and gas chromatography using a Flash EA1112 (Thermo Scientific, Waltham, MA, USA) total element analyser.

Solid state ^{13}C CPMAS NMR spectroscopy

Solid state ^{13}C NMR spectroscopy was used to determine the proportions of aliphatic, carbohydrate and aromatic C (Baldock & Preston, 1995). Peat samples were taken from 0 to 10, 90 to 100 and 170 to 190 cm depth (the depth of the deepest sample varied slightly between sites), while at the sawgrass site samples from 50 to 60 cm depth were also analysed. None of these samples contained macroscopic charcoal which, if present at high concentrations, can influence the measurement. NMR spectra were obtained using a DSX200 spectrometer (Bruker, Coventry, UK) equipped with double-bearing probes for cross polarization and magic angle spinning. The resonance frequency for ^{13}C was 50 MHz and the sample was spun at the magic angle with a speed of 7 kHz. The contact time and relaxation delay for the cross polarization technique were 2.0 ms and 3.0 s, respectively, with 20000 scans accumulated for high-power ^1H decoupling. All spectra were determined at ambient temperature and processed with a line-broadening factor of 50 Hz. Chemical shifts were calibrated using an external sample of tetrakis(trimethylsilyl)silane. The CP method, although sensitive, tends to overestimate the proportion of aliphatic C, although this effect is pronounced only in materials with a high proportion of polyaromatic C such as lignite and coal (Love *et al.*, 1992). This effect should not be significant for peat, which has only 5–10% aromatic C, most of which is not polyaromatic. The NMR-derived C concentration was calculated based on the total C content of the peat.

Statistical analysis

The results were analysed using Genstat version 13 (Lawes Agricultural Trust, Rothamsted Experimental Station, UK). *In*

situ CO_2 and CH_4 fluxes were analysed using a repeated measures ANOVA structure with site, depth and time as fixed effects. As significant interactions with time were found, the effects of site and depth were analysed separately for each month. *Ex situ* CO_2 and CH_4 flux measurements and peat properties were analysed using two separate ANOVAs. The first analysis included the replicated samples to a depth of 1 m for all three sites, with site and depth as fixed effects, while the second tested for depth effects for the three 2 m deep cores (i.e. one from each site). Because of the disturbance of the top 0–30 cm of the cores, the mean values for additional 10 cm deep surface cores collected for all sites were used as the '5 cm' depth point in the analysis. Mean values and standard errors of the mean are reported. All data were tested for normality and transformed if necessary to meet the normality assumption in the ANOVA. Statements made in the Results section are underpinned by statistical summaries presented in the figure legends. Owing to the unreplicated nature of the solid state ^{13}C CPMAS NMR data, only limited statistical analysis could be carried out for these results.

Results

Peat properties

Gravimetric moisture content was extremely high throughout the profile, ranging from 89 to 99% (Fig. 2a). pH ranged from 3.5 to 4.5 (Fig. 2b) and was highest in the surface peat layer, decreased sharply at 40 cm depth, and then remained relatively constant through the profile apart from at the *C. panamensis* site, where pH increased slowly from the surface minimum to a depth of 1 m. The peat was generally weakly reduced throughout the profile (Fig. 2c), with mean redox potentials for the entire profile of 282, 335 and 356 mV at the *R. taedigera*, *C. panamensis* and *Cyperus* sites, respectively.

LOI was generally extremely high, ranging between 82% and 99%, except for distinct layers of higher ash content at depths of 110–140 and 150 cm at the *R. taedigera* and *C. panamensis* sites (Fig. 2d). Dry BD was very low and always $<0.09 \text{ g cm}^{-3}$ (Fig. 2e). The BD of the surface peat (0–10 cm) was lowest at the *Cyperus* site (ca. 0.02 g cm^{-3}), but the values for depths of 10–120 cm were generally similar, ranging from 0.03 to 0.05 g cm^{-3} at all sites, although a marked increase was apparent between 120 and 140 cm at the *R. taedigera* and *C. panamensis* sites. The peak in BD at the *R. taedigera* site corresponded to a much lower LOI and a high pH for the same depth.

Root dry biomass did not vary significantly with depth within the upper 100 cm and was close to zero at depths $>110 \text{ cm}$ (Fig. 2f). The values were greatest at the *Cyperus* site for depths between 0 and 65 cm, with maximum values of ca. 360 g m^{-2} . However, at greater

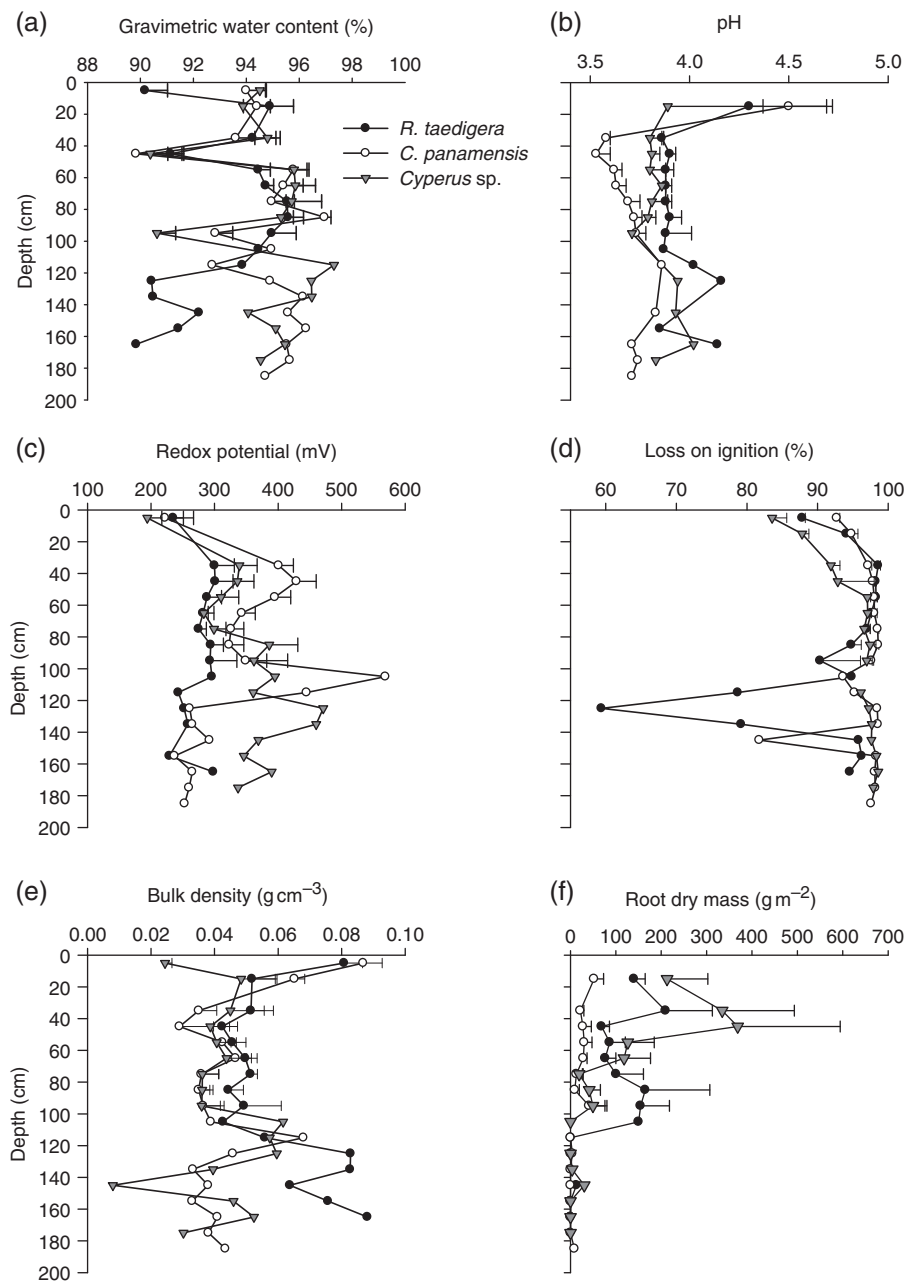


Fig. 2 Profiles of peat properties to a depth of 2 m for each site; $n = 5$ for 0–10 cm, $n = 4$ for 10–100 cm and $n = 1$ for 100–200 cm. Single standard errors of the mean are shown for depths of 0–100 cm. ANOVA outputs to a depth of 100 cm are: (a) gravimetric soil moisture content, Depth: $F_{8,108} = 7.32$, $P < 0.001$; Site: $F_{2,108} = 4.18$, $P = 0.019$; Site \times Depth: $F_{16,108} = 8.31$, $P < 0.001$; (b) pH, Depth: $F_{8,84} = 5.62$, $P < 0.001$; Site: $F_{2,84} = 29.13$, $P < 0.001$; Site \times Depth: $F_{16,84} = 1.05$, $P = 0.422$; (c) redox potential, Depth: $F_{8,110} = 10.63$, $P < 0.001$; Site: $F_{2,110} = 9.78$, $P < 0.001$; Site \times Depth: $F_{16,110} = 1.36$, $P = 0.180$; (d) loss on ignition, Depth: $F_{8,109} = 12.73$, $P < 0.001$; Site: $F_{2,109} = 11.46$, $P < 0.001$; Site \times Depth: $F_{16,109} = 2.35$, $P < 0.01$; (e) bulk density, Depth: $F_{8,110} = 6.28$, $P < 0.001$; Site: $F_{2,110} = 11.36$, $P < 0.001$ and Site \times Depth: $F_{16,110} = 4.12$, $P < 0.001$ and (f) root biomass, Depth: $F_{7,95} = 1.60$, $P = 0.15$; Site: $F_{2,95} = 2.79$, $P = 0.11$; Depth \times Site: $F_{14,95} = 1.44$, $P = 0.16$. Single cores ($n = 1$ at each site) 15–185 cm, Depth: $F_{16,47} = 1.96$, $P = 0.056$.

depths (75–105 cm), root biomass was greatest at the *R. taedigera* site, although the values were distinctly lower (150 g m^{-2}) than in the surface layers at the *Cyperus* site. Root biomass was consistently lowest for *C. panamensis* throughout the profile.

The concentrations of DOC and TDN varied significantly among sites, with the highest concentrations being recorded at the *R. taedigera* site and the lowest at the *Cyperus* site (Fig. 3). Neither DOC nor DN varied significantly with depth.

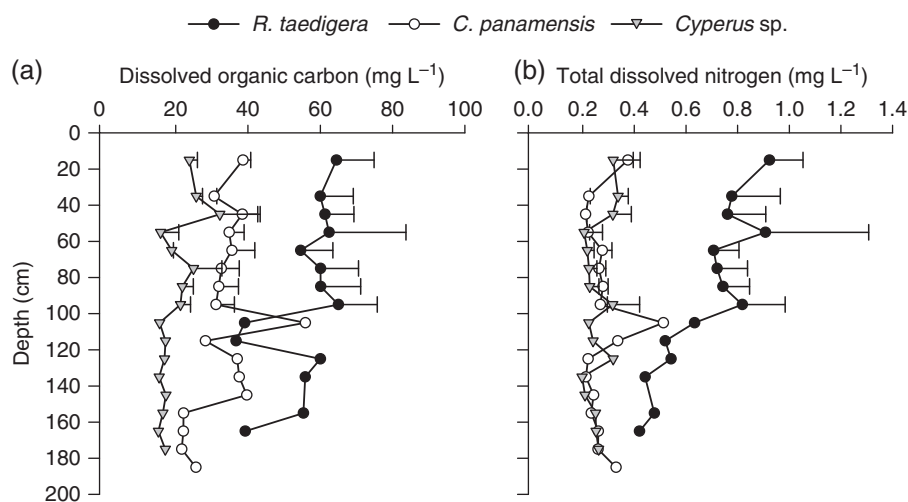


Fig. 3 Profiles of dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) to a depth of 2 m for each site; $n = 4$ for 10–100 cm, $n = 1$ for 100–200 cm. Single standard errors of the mean are shown for depths of 0–100 cm, ANOVA summaries to a depth of 100 cm are: (a) DOC, Depth: $F_{7,95} = 0.30$, $P = 0.95$; Site: $F_{2,95} = 56.20$, $P < 0.001$; Site \times Depth: $F_{14,95} = 0.21$, $P = 0.99$; (b) DN, Depth: $F_{7,95} = 0.44$, $P = 0.88$; Site: $F_{2,95} = 69.79$, $P < 0.001$; Site \times Depth: $F_{14,95} = 0.45$, $P = 0.95$.

Solid state CPMAS ^{13}C NMR spectroscopy

Clear changes in peat chemistry with depth were observed (Table 1; Fig. 4). The marked increase in the ratio of aromatic C to carbohydrate and distinct decreases in the relative intensity of chemical shifts associated with polysaccharide resonances at 106, 72 and 64 ppm indicate carbohydrate decay. By contrast, the ratio of carbohydrates to aliphatic compounds showed no clear trend with depth. Another distinct trend at all sites was a decrease in the methoxyl to aromatic C ratio with depth.

The most pronounced difference between sites was the greater quantity of carbohydrates found throughout the profile at the *Cyperus* site. Overall, the mean proportion of labile C present as carbohydrate (spectral range 50–110 ppm) averaged across the entire profiles for all three sites was 21%. The values were greatest at the *Cyperus* site, near the centre of the peatland (25%), followed by the *C. panamensis* and *R. taedigera* sites (19% and 18%, respectively).

In the aromatic region of the spectrum, peaks at 135, 148 and 153 ppm are assigned to C bound to oxygen and/or other C atoms in the stable part of the aromatic lignin structure (Fig. 4). This component of the lignin structure remained unaltered with respect to depth in all cores, indicating that the aromatic C in lignin is stable.

In situ fluxes of CO_2 and CH_4

CO_2 fluxes did not vary significantly between sites or with depth when the combined data for all sites sampled in July 2008 were analysed (Fig. 5a–c). How-

ever, in August, CO_2 fluxes (Fig. 5d–f) were greatest for the surface horizon at all three sites, ranging from 320–500 $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$. Fluxes from the surface layer were two to three-fold higher than at 30 cm or greater depths and the values were comparable for all sites. The contrasting patterns for CO_2 fluxes between months are reflected by the significant Month \times Depth interaction ($F_{3,67} = 3.97$; $P < 0.05$) resulting from the greatly increased surface efflux in August at the *C. panamensis* and *Cyperus* sites.

There was no significant difference in CH_4 fluxes among sites in July (Fig. 6a–c), although a significant depth effect was found across all three sites, with emissions being greatest 30 cm below the surface. CH_4 fluxes were very low at depths > 30 cm at the *R. taedigera* and *C. panamensis* sites, but detectable fluxes were apparent at 60 and 100 cm at the *Cyperus* site. In August, CH_4 fluxes were greatest from the surface layer at the *R. taedigera* and *C. panamensis* sites and values for the deeper layers were very low (Fig. 6d–f). However, no significant variation with depth was found for the *Cyperus* site and the flux from the surface layer was much lower than at the other two sites. The influence of time on the depth distribution of CH_4 fluxes was significant (Month \times Depth: $F_{3,76} = 5.79$; $P = 0.002$).

At the time of sampling in July and August 2008, neither water table nor substrate temperature varied significantly among sites. Cumulative rainfall during the preceding month was also similar, being 322 and 362 mm in July and August, respectively. The water table tended to be just below the peat surface (average of 8 cm) at the *R. taedigera* site and just above the surface (average of 6 cm) at the two sites closer to the interior of

Table 1 Composition of material from peat cores collected from three contrasting vegetation communities based on ^{13}C solid state CPMAS NMR

Site	Depth (cm)	C (mg g ⁻¹)	Aliphatic (0–50)	Methoxyl (50–60)	Carbohydrate (60–90)	Carbohydrate + Aliphatic lignin (90–110)	Aromatic lignin (110–160)	Carboxyl-Carbonyl (160–200)	Methoxyl/Aromatic	Aromatic/Aliphatic	Carbohydrate/Aliphatic	Aromatic/Carbohydrate
<i>Raphia taedigera</i>	5	489	236 (43.8)	23 (4.8)	117 (24.0)	23 (4.8)	54 (11.0)	35 (7.2)	0.44	0.23	0.50	0.46
	95	566	177 (31.2)	38 (6.6)	130 (22.9)	38 (6.6)	147 (25.9)	38 (6.6)	0.26	0.83	0.73	1.13
	175	387	94 (24.3)	31 (7.9)	104 (27.0)	33 (8.6)	109 (28.3)	15 (3.9)	0.28	1.16	1.11	1.05
<i>Camposperma panamensis</i>	5	485	168 (34.6)	31 (6.3)	142 (29.2)	35 (7.3)	74 (15.3)	35 (7.3)	0.41	0.44	0.85	0.52
	95	528	183 (34.7)	28 (5.3)	125 (23.7)	35 (6.7)	118 (22.3)	39 (7.3)	0.24	0.64	0.68	0.94
	185	527	172 (32.7)	33 (6.3)	116 (22.0)	30 (5.7)	127 (24.0)	49 (9.3)	0.26	0.73	0.67	1.09
<i>Cyperus</i> sp.	5	424	107 (25.3)	26 (6.1)	183 (43.2)	39 (9.1)	43 (10.1)	26 (6.1)	0.60	0.40	1.71	0.23
	55	501	86 (17.2)	25 (5.0)	227 (45.4)	60 (11.9)	86 (17.2)	17 (3.3)	0.29	1.00	2.63	0.38
	95	545	150 (27.4)	29 (5.4)	159 (29.1)	40 (7.4)	117 (21.4)	51 (9.4)	0.25	0.78	1.06	0.74
	173	555	160 (28.8)	33 (6.0)	149 (26.8)	39 (7.0)	124 (22.4)	50 (9.0)	0.27	0.78	0.93	0.84

Functional groups associated with specific spectral ranges (ppm) are shown as NMR-derived C concentrations in the samples (mg g⁻¹); values in brackets are the proportion (%) of each C fraction based on total C content. The concentration ratios between functional groups are shown to illustrate their relative distribution within the peat profiles. Values represent single measurements for each depth at each site.

the peatland (Table 2). However, rainfall during the 24 h period preceding sampling rapidly and substantially affected the height of the water table by up to 10–15 cm (E. L. Wright, personal observation).

Ex situ CO₂ and CH₄ emissions

Peat from the *C. panamensis* and *Cyperus* sites tended to respire more rapidly to a depth of ca. 40 cm than that from the *R. taedigera* site when expressed on a unit peat mass basis, with a maximum CO₂ production of ca. 0.07 mg CO₂ g⁻¹ h⁻¹ for both the *C. panamensis* and *Cyperus* sites (Fig. 7a). Below that depth, CO₂ fluxes at the *R. taedigera* site were greater than at the *C. panamensis* and *Cyperus* sites, with a peak of 0.075 mg CO₂ g⁻¹ h⁻¹ at 55 cm depth. There was a second peak in CO₂ emissions between 120 and 150 cm at all three sites. CO₂ production expressed on a unit land area basis was greatest for *R. taedigera* in the top 1 m of peat, reflecting the higher BD of peat at this site (Figs. 7c and 2e). CO₂ fluxes peaked at 120–160 cm depth at all sites, with maximum values of ca. 370, 280 and 230 mg CO₂ m⁻² h⁻¹ being obtained for *C. panamensis*, *R. taedigera* and *Cyperus*, respectively (Fig. 7c).

CH₄ fluxes expressed on a peat dry mass basis were significantly greater for the *R. taedigera* and *Cyperus* sites at depths of 0–130 cm (Fig. 7b), with maximum recorded fluxes of 0.0010 and 0.0018 mg CH₄ g⁻¹ h⁻¹, respectively. When expressed per unit land area, CH₄ fluxes were significantly greater at the *R. taedigera* and *Cyperus* sites than at the *C. panamensis* site, with a maximum value of ca. 7 mg CH₄ m⁻² h⁻¹ being recorded at the *R. taedigera* site (Fig. 7d).

Cumulative CO₂ fluxes (i.e. the sum of fluxes measured from the individual 10 cm segments in the *ex situ* study) to a depth of 1.6 m were, respectively, 2600, 2400 and 2200 mg CO₂ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sites. Cumulative CH₄ fluxes showed greater variation among sites, being greatest for *R. taedigera* followed by *Cyperus* and *C. panamensis* (39, 26 and 11 mg CH₄ m⁻² h⁻¹, respectively). Cumulative CO₂ and CH₄ fluxes were an order of magnitude greater than the surface fluxes measured at the time of coring. Surface CO₂ and CH₄ fluxes measured at the same sites in November 2007 were 202 ± 46, 104 ± 54 and 289 ± 44 mg CO₂ m⁻² h⁻¹, and 1.03 ± 0.87, -0.27 ± 0.39 and 1.12 ± 0.39 mg CH₄ m⁻² h⁻¹ for the *R. taedigera*, *C. panamensis* and *Cyperus* sites, respectively.

Percentage moisture content and BD of the peat at each site and depth examined accounted for 33% and 26%, respectively, of the variation in CO₂ fluxes (Fig. 8a and b), with CO₂ fluxes being greater for peat with a high moisture content and low BD. In contrast, CH₄ fluxes were not correlated with either moisture content

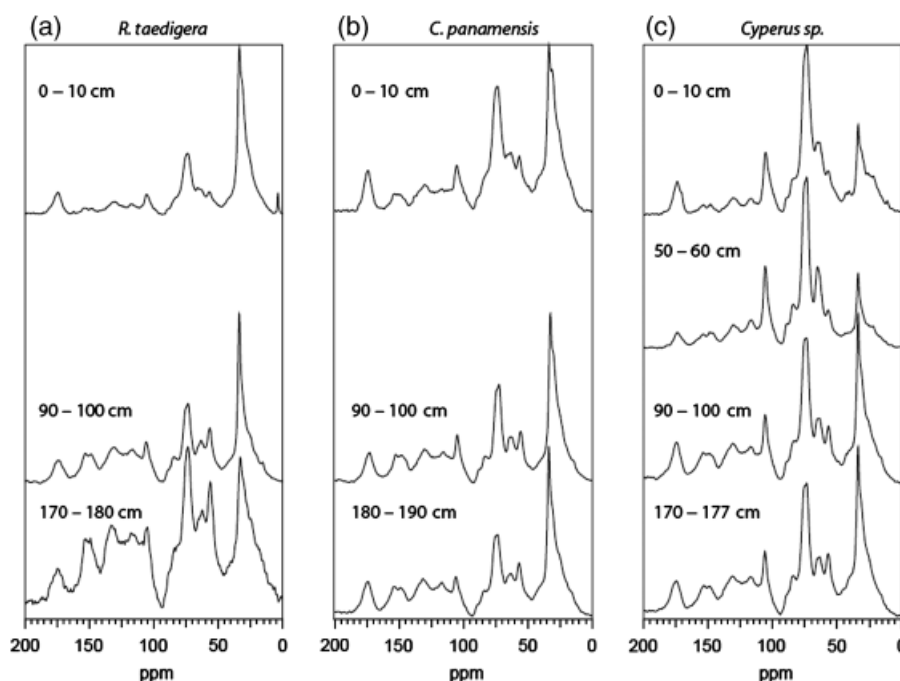


Fig. 4 ^{13}C solid state MAS NMR spectra for depths of 0–10, 50–60*, 90–100 and 170–180 cm for: (a) *R. taedigera*; (b) *C. panamensis* and (c) *Cyperus* sp. **Cyperus* site only.

or BD (data not shown). Redox potential, root biomass, DOC and TDN did not contribute significantly to the observed variation in CO_2 and CH_4 fluxes.

In addition to the relationship between CO_2 fluxes and the physical properties of the peat, there were strong positive relationships between CO_2 and CH_4 fluxes and the quantity of labile C present in the peat (Fig. 9). CO_2 emissions were most strongly predicted by the ratio of carbohydrate to aliphatic functional groups (indicating the degree of decomposition), accounting for 30% of the variance, while 63% of the variation in CH_4 fluxes was attributable to the concentration of carbohydrates (60–90 ppm) in the peat.

Discussion

In contrast to SE Asia (Couwenberg *et al.*, 2010), the *in situ* and *ex situ* measurements both show clearly that the deeper peat layers may contribute substantially to the net efflux of CO_2 from the peatland examined here. The *in situ* measurements showed that subsurface CO_2 production made a greater contribution to net CO_2 emissions from the top 30 cm in August than in July (Fig. 5). This shift in CO_2 emissions suggests the occurrence of strong temporal variability despite the permanently high water table and stable peat temperature, in sharp contrast to findings in SE Asia where fluctuations in the water table were the main driver of temporal variation in CO_2 fluxes (Jauhiainen *et al.*, 2005; Melling

et al., 2005a,b; Hirano *et al.*, 2007). Measurements extending over longer time periods and with greater temporal resolution are needed to establish the factors controlling temporal variability in CO_2 fluxes in the San San Pond Sak peatland.

The high cumulative CH_4 efflux from the *ex situ* peat cores highlights the potential for substantial emissions of this potent greenhouse gas from tropical peatlands, although the relatively low *in situ* net emissions from the peat surface in July, despite substantial production at a depth of 30 cm (Fig. 6), suggests strong oxidation of CH_4 in the surface peat. In August, CH_4 emissions from the surface peat were much greater and within the upper range of values reported for SE Asian peatlands (Couwenberg *et al.*, 2010). This suggests that the peatland can switch rapidly from being a weak to a strong source of CH_4 and highlights that, as for CO_2 , strong variation in CH_4 emission can occur without variation in the water table or peat temperature. The depth distribution of CO_2 and CH_4 fluxes did not vary greatly among sites, suggesting that gas production does not depend directly on the properties of distinct vegetation communities, such as the nutrient status of the litter produced (Troxler, 2007; Sjögersten *et al.*, 2010).

The large *ex situ* gas fluxes relative to the *in situ* fluxes may well reflect the slow gas diffusion through the water-saturated peat profile *in situ*. High gas concentrations at depth in peat profiles have been recorded previously in tropical peatlands (e.g. Inbushi *et al.*,

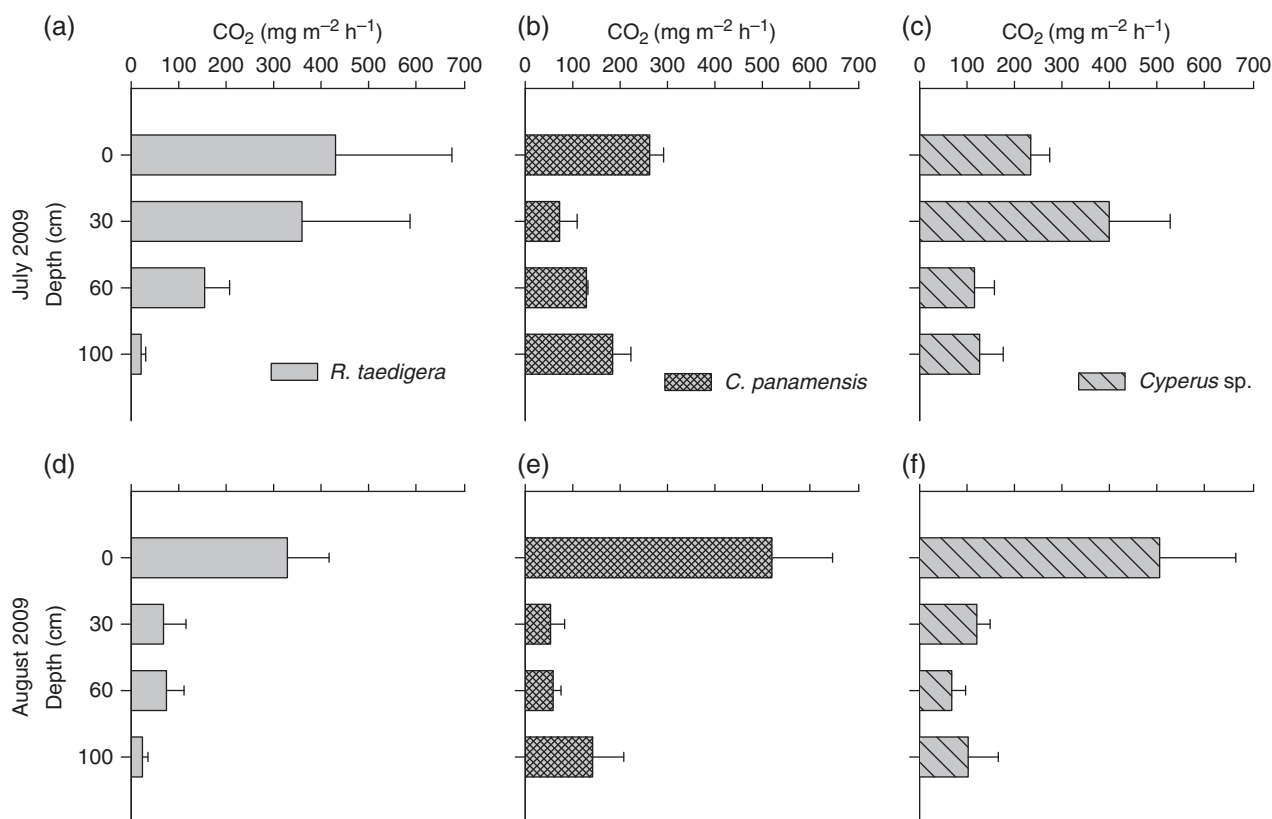


Fig. 5 Mean *in situ* CO₂ fluxes during July (a–c) and August 2009 (d–f) at the *R. taedigera*, *C. panamensis* and *Cyperus* sites. Fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown ($n = 4$). ANOVA summaries for July are: Depth, $F_{3,32} = 0.79$, $P = 0.52$; Site, $F_{2,32} = 0.23$, $P = 0.79$, and for August are: Depth, $F_{3,42} = 18.43$, $P < 0.001$; Site, $F_{2,42} = 0.49$, $P = 0.62$.

1998; Melling *et al.*, 2005a). The *ex situ* fluxes reported here should therefore be interpreted as potential fluxes following removal of the hydraulic head, rather than a measure of the actual contribution of individual peat layers to surface emissions. The release of CH₄ from deep peat layers to the atmosphere is likely to be mediated both by the dominant vegetation (Joabsson & Christensen, 2001) and ebullition, which is known to be an important transport mechanism for the release of CH₄ in northern peatlands (Comas *et al.*, 2007).

The high *in situ* CO₂ fluxes in August suggest substantial losses of C from the peatland if extrapolated to an annual timescale. Such large C losses must be balanced by similarly high gross net primary productivity to maintain the C accumulation rates estimated by Phillips *et al.* (1997). High tree basal areas have been reported for the *R. taedigera* and *C. panamensis* sites (Sjögersten *et al.*, 2010), but further work on their productivity and C allocation is needed to determine the C balance of the peatland. Indeed, substantial below ground inputs of labile C from the trees might be an important contributor to the high *in situ* CO₂ and CH₄ fluxes, analogous to the reports of strong direct

controls of gas production by the vegetation in northern peatlands (Joabsson & Christensen, 2001).

The strong relationship between C fluxes and peat composition (Fig. 9) suggests that CO₂ and CH₄ production were substrate-limited to a depth of 2 m as fluxes of these gases depend on the type and quantity of carbohydrates present. The greater CO₂ and CH₄ fluxes in the surface peat at the *Cyperus* sites (Fig. 7) are likely to be related to the greater quantities of carbohydrates in the peat. The greater lability of peat at the *Cyperus* site is reflected by its higher microbial biomass C content and extracellular enzyme activity (e.g. cellobiohydrolase, xylanase, glucosidase) in the surface peat compared with sites closer to the edge of the peatland (Sinsabaugh *et al.*, 2008; Sjögersten *et al.*, 2010). The accumulation of deep carbohydrate-rich peat at the *Cyperus* sites may reflect nutrient limitation of the heterotrophic microbial community, resulting in slow decomposition and preservation of carbohydrates (Phillips *et al.*, 1997; Sjögersten *et al.*, 2010). In contrast, the *R. taedigera* peat had relatively high CH₄ release despite low carbohydrate concentrations; however, this site has higher substrate nutrient levels (Sjögersten *et al.*, 2010).

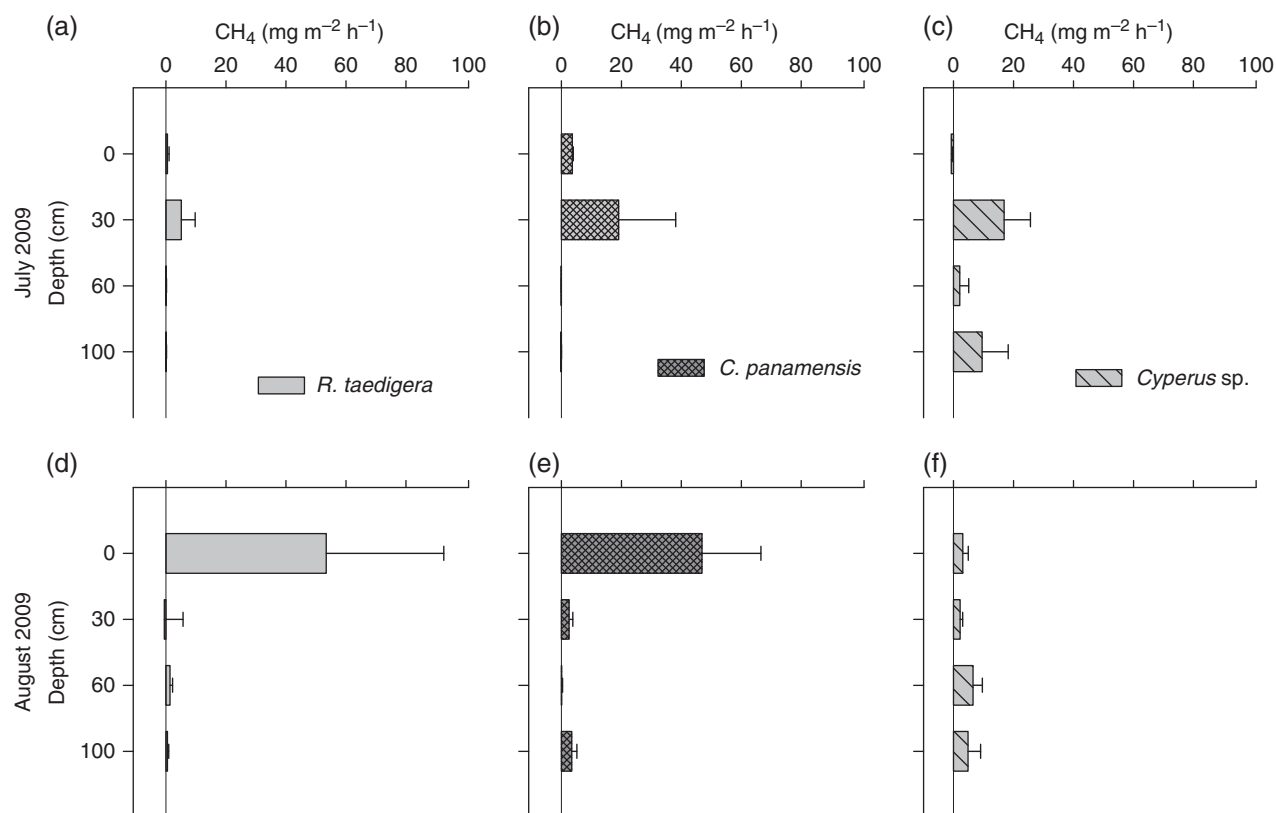


Fig. 6 Mean *in situ* CH₄ fluxes during July (a–c) and August 2009 (d–f) at the *R. taedigera*, *C. panamensis* and *Cyperus* sites. The fluxes shown for specific depths represent gas production from the base of the sampling tube up to that depth in the profile. Single standard errors of the mean are shown ($n = 4$). ANOVA summaries for July were: Depth, $F_{3,37} = 4.55$, $P < 0.05$; Site, $F_{2,37} = 0.48$, $P = 0.63$, and for August were Depth, $F_{3,46} = 6.45$, $P < 0.01$; Site, $F_{2,46} = 0.37$, $P = 0.70$.

Table 2 Water table and peat temperature for all sites measured concurrently with the *in situ* gas sampling ($n = 4$)

	Water table (cm) July	Water table (cm) August	Soil temperature (°C) July	Soil temperature (°C) August
<i>Raphia taedigera</i>	-13.9 ± 0.7	-2.3 ± 1.4	25.2 ± 0.3	25.8 ± 0.9
<i>Campnosperma panamensis</i>	6.8 ± 0.6	1.3 ± 2.1	24.8 ± 0.2	25.0 ± 0
<i>Cyperus sp.</i>	5.2 ± 0.3	10.0 ± 1.3	26.6 ± 0.7	27.2 ± 2.2

Means and SEM are shown. Negative values indicate depth of water table below the ground surface.

and DOC and TDN concentrations, which may contribute to the overall higher emissions from this site. The *R. taedigera* site exhibited the greatest cumulative CO₂ and CH₄ emissions per unit land area to a depth of ca. 1.6 m due to the combination of the high lability and slightly greater density of the peat.

Approximately 30% of the peat C in San San Pond Sak was present in the form of carbohydrate compounds which are considered to be readily accessible for microbial degradation. The solid state ¹³C NMR results clearly indicate progressive decay of carbohydrates relative to lignin with depth at all three sites, as indicated by the systematic decrease of the carbohydra-

te:lignin ratio (Fig. 4; Table 1) and the decreasing methoxyl:aromatic ratio resulting from microbial cleavage of aromatic methoxyl moieties (Vane *et al.*, 2003). Compared with other peatlands (Krull *et al.*, 2004; Grover & Baldock, 2010), the proportion of carbohydrates (at chemical shifts 60–110 ppm) in the surface peat was low (117–183 mg g⁻¹), while the proportion of aliphatic C (at chemical shifts 0–50 ppm) was comparatively high (107–236 mg g⁻¹) (Table 1). This suggests either a rapid initial loss of carbohydrates and that the surface peat material was already depleted of labile C, or that aliphatic C is an important component of the C inputs. The relative decay of lignin and cellulose there-

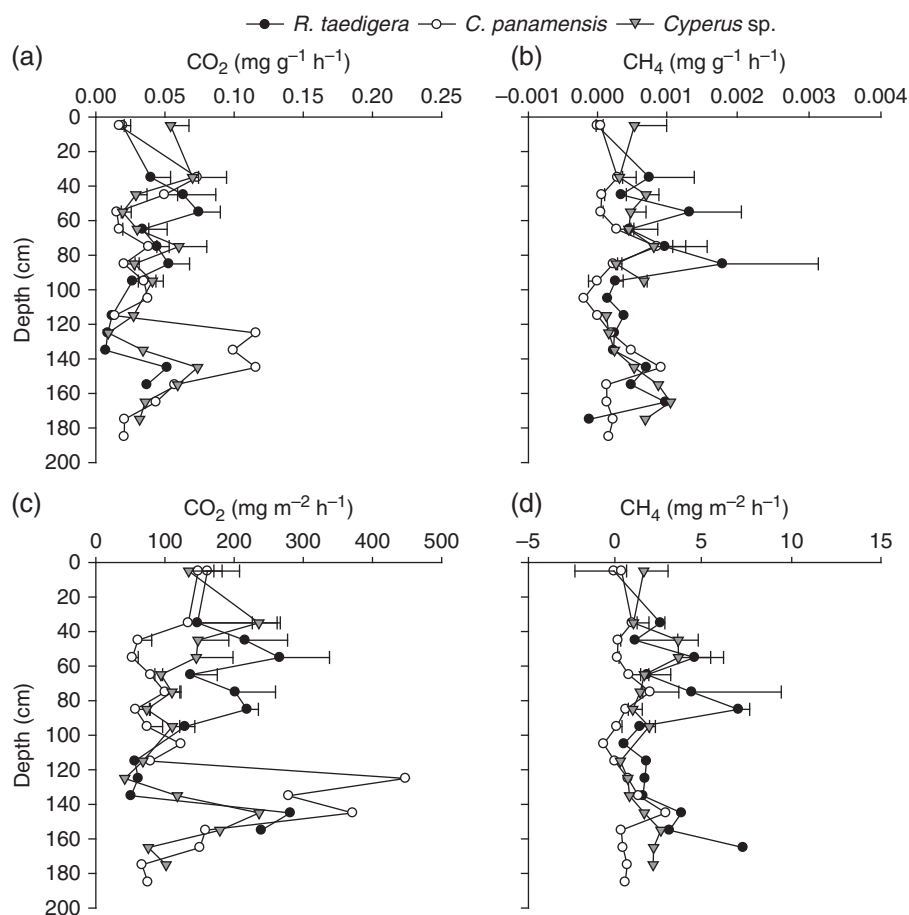


Fig. 7 Fluxes of CO_2 (a, c) and CH_4 (b, d) expressed on the basis of peat mass (a, b) and land surface area (c, d) throughout the profile. Single standard errors of the mean are shown for depths ≤ 100 cm ($n=5$ for 0–10 cm and $n=4$ for 10–100 cm). Values for depths >100 cm are unreplicated. ANOVA summaries for 5–95 cm were: (a) Depth: $F_{7,83} = 3.78$, $P = 0.002$; Site: $F_{2,83} = 3.49$, $P < 0.05$; Site \times Depth: $F_{14,83} = 3.71$, $P < 0.001$; (b) Depth: $F_{7,85} = 1.51$, $P = 0.18$; Site: $F_{2,85} = 4.38$, $P < 0.05$; Site \times Depth: $F_{14,85} = 1.36$, $P = 0.20$; (c) Depth: $F_{7,83} = 1.65$, $P = 0.138$; Site: $F_{2,83} = 10.13$, $P < 0.001$; Site \times Depth: $F_{14,83} = 1.92$, $P < 0.05$; (d) Depth: $F_{7,85} = 1.42$, $P = 0.21$; Site: $F_{2,85} = 6.29$, $P < 0.01$; Site \times Depth: $F_{14,85} = 1.62$, $P = 0.10$. ANOVA summaries for 5–185 cm (one core from each site) were: (a) Depth: $F_{16,53} = 1$, $P < 0.05$; (b) Depth: $F_{16,55} = 0.93$, $P = 0.5$; (c) Depth: $F_{16,53} = 1.24$, $P = 0.28$; (d) Depth: $F_{16,55} = 0.89$, $P = 0.59$.

fore provides a more reliable measure of decomposition than ratios involving aliphatic compounds, as has also been shown for subtropical (Orem & Hatcher, 1986; Krull *et al.*, 2004), alpine (Grover & Baldock, 2010) and subarctic communities (Sjögersten *et al.*, 2003).

The higher cellulose content of peat at the *Cyperus* site is comparable to the shifts in the organic chemistry of peat with depth and between peatland vegetation communities found in domed peat deposits in Sarawak, Malaysia (Calvert *et al.*, 1991). In Sarawak, the highest cellulose content was associated with peat under herbaceous vegetation, while deeper peat and peat formed from woody vegetation showed strong signals from lignin (Calvert *et al.*, 1991; Orem *et al.*, 1996). Deep peat layers in tropical bogs in Kalimantan, Borneo have undergone substantial microbial degradation (Dehmer,

1993), suggesting that it is peat located closer to the surface that contributes most to gas emissions. Peat from San San Pond Sak produced both CO_2 and CH_4 to a depth of 2 m *ex situ* and the values did not decline strongly with depth, indicating that the peat was relatively labile throughout this depth range. The NMR data indicate that decomposition was lower than that of surface peats in Indonesia which had a low carbohydrate content (9%; Orem *et al.*, 1996). The NMR data and high gas fluxes suggest that peat in San San Pond Sak is labile to greater depth than in SE Asia (Orem *et al.*, 1996; Melling *et al.*, 2005a). We speculate that the permanently high water table in the wetland examined here limits decomposition to a greater extent than in SE Asia, where greater draw-down of the water table occurs (e.g. Jauhainen *et al.*, 2005).

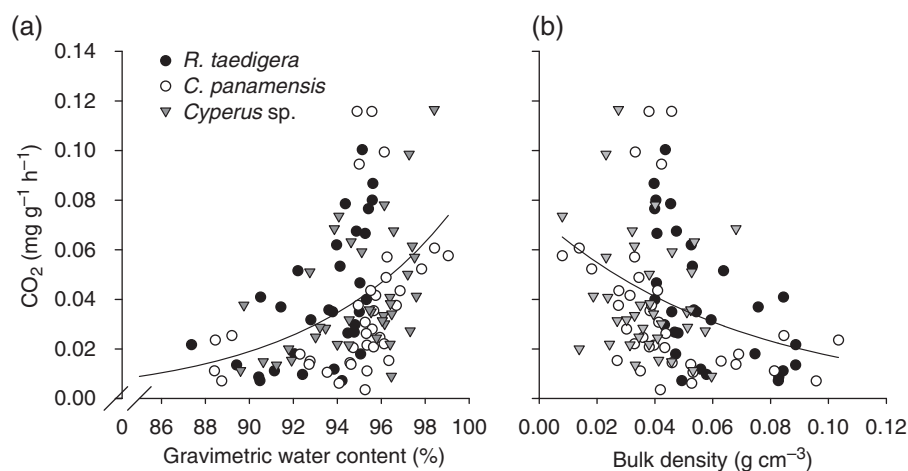


Fig. 8 Relationship between CO_2 flux and (a) percentage moisture content; $F_{1,114} = 58.06$, $P < 0.001$ and (b) bulk density of peat, $F_{1,115} = 41.14$, $P < 0.001$.

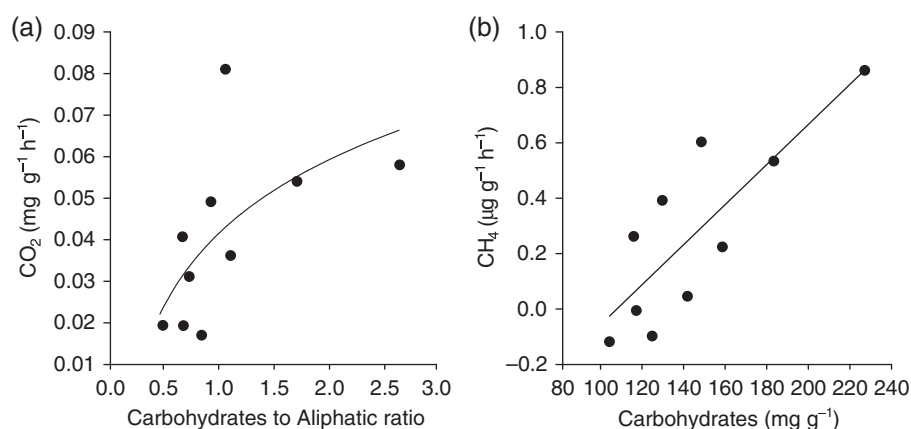


Fig. 9 Relationship between *ex situ* CO_2 fluxes and: (a) the ratio between carbohydrates and aliphatic C (log-linear regression: $F_{1,8} = 4.85$, $P = 0.059$, variance explained 30%); and (b) the carbohydrate content of the peat (linear regression: $F_{1,8} = 16.40$, $P < 0.01$, variance explained 63%).

With respect to the relationships between CO_2 fluxes, BD and soil moisture content (Fig. 8), we speculate that these reflect to some extent either substrate lability, i.e. the relatively low density peat at the *Cyperus* site tended to be more carbohydrate-rich, or that supplies of O_2 and labile DOC (Charman *et al.*, 1994) to depth through highly permeable peat stimulated respiration. However, the measured profiles for DOC (Fig. 3) did not provide reliable predictions of gas production. The density of peat was generally low and within the range reported for tropical peatlands (Shimada *et al.*, 2001; Page *et al.*, 2004; Lahteenoja *et al.*, 2009). It is also interesting to note that BD did not change consistently with depth to 2 m. Similarly, BD was low throughout the profile in peatlands in Kalimantan to a depth of 9 m and in some peats in the Amazon to depths of 4.9 m (Page *et al.*, 2004; Lahteenoja *et al.*, 2009). These observations suggest that

low BD may be an important feature of tropical peatlands compared with the denser peat found at depth in temperate and boreal peatlands (Laiho *et al.*, 2004; Danevčič *et al.*, 2010).

Redox potential did not explain the variation in CO_2 and CH_4 fluxes from peat cores from the San San Pond Sak peatland. Similarly, spatial variation in CO_2 and CH_4 fluxes under field conditions have been found to be independent of redox potential (Ueda *et al.*, 2000; Chimner & Ewel, 2004; Hadi *et al.*, 2005), suggesting that other soil properties, such as nutrient status, are more important drivers (Wright & Reddy, 2001; Hadi *et al.*, 2005; Yu *et al.*, 2007). However, the relatively high redox potentials observed throughout the profile to a depth of 2 m and the high root biomass down to ca. 110 cm (Fig. 2) may have been at least partly responsible for the large gas production in the subsurface peat (Figs.

5–7; Bergman *et al.*, 1999; Metcalfe *et al.*, 2007; Yu *et al.*, 2007; Seo & Dehaune 2010).

Climate change predictions for Panama suggest an increase in air temperature of up to 3.5 °C and a reduction in precipitation (Meehl *et al.*, 2007), potentially lowering water tables in the peatland. As water table draw-down has been shown to increase CO₂ emissions from SE Asian peatlands (Jauhiainen *et al.*, 2005; Hirano *et al.*, 2009), it is plausible that any reduction in water table resulting from climate change would increase CO₂ emissions from San San Pond Sak, a view supported by the increased CO₂ fluxes from experimentally drained surface peat from the site (Sjögersten *et al.*, 2010). The potential fluxes of CO₂ and CH₄ to a depth of 2 m (Fig. 7) suggest that the deeper layers of peatlands may contribute substantially to increased CO₂ and CH₄ emissions in response to elevated temperature (Hirano *et al.*, 2009; Long *et al.*, 2010). Draw-down of the water table would reduce the extent of the anaerobic microsites in the upper 30 cm of the peat profile that currently are most active in producing CH₄ (Fig. 6). The combined effect of the lower quality of peat at depth (Table 1) and a thicker surface layer of aerated peat where oxidation of CH₄ takes place would be likely to reduce CH₄ emissions from this neotropical peatland.

In conclusion, detailed knowledge of the processes affecting gas production from deep peat layers is essential to predict how climate change will affect the net fluxes of CO₂ and CH₄ from tropical peatlands. Moreover, it is clear that deeper peat layers have the potential to lose C rapidly, and that variation in peat quality and BD within the profile associated with contrasting vegetation communities in tropical peatlands is important in determining CO₂ and CH₄ production. There is currently a dearth of information regarding the sources of CO₂ and CH₄ within peat profiles, the environmental constraints on the release of the gases produced and the influence of vegetation type on both the production and release of these gases. Further work, including radiocarbon dating of DOC, CO₂ and CH₄ gases and more intensive measurements of gas emissions in relation to the role of the vegetation and abiotic variables is needed to fill the knowledge gaps which currently limit our ability to predict CO₂ and CH₄ emissions from neotropical peatlands. Such studies are vital in view of the substantial land areas occupied by such systems and their considerable potential contribution to future climate change.

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